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Plate I.

"*Natura infinita est; sed qui symbola animadverterit omnia intelliget, licet non omnino*".

Goethe.

R. Owen, del. J. Erxleben, on Stone.

Day & Son, Lith.rs to the Queen.

75941

ON

PARTHENOGENESIS,

OR

THE SUCCESSIVE PRODUCTION OF

PROCREATING INDIVIDUALS

FROM

A SINGLE OVUM.

A DISCOURSE

INTRODUCTORY TO THE HUNTERIAN LECTURES ON
GENERATION AND DEVELOPMENT,
FOR THE YEAR 1849,

DELIVERED AT THE

ROYAL COLLEGE OF SURGEONS OF ENGLAND.

BY

RICHARD OWEN, F.R.S. &c.,

HUNTERIAN PROFESSOR AND CONSERVATOR OF THE MUSEUM.

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ON

PARTHENOGENESIS.

THERE is a natural and irrepressible tendency in the human mind to penetrate the mystery of the beginning of things, and above all that of the origin of living things, involving our own origin.

But it is plainly denied to finite understandings to ascend to the very beginning, and to comprehend the nature of the operation of the First Cause of anything.

And perhaps the best argument from reason for a future state and the continued existence of our thinking part, is afforded by the fact of our being able to conceive the possibility of the enjoyment of such knowledge, and the consequent yearning to possess it,—that *μάντευμα τι* of Plato, or parturient vaticination of some higher knowledge which cannot be fulfilled in the present state of our existence.

The ablest endeavours here to penetrate to the beginning of things do but carry us, when most successful, a few steps nearer that beginning, and then leave us on the verge of a boundless ocean of the unknown truth, dividing the secondary or subordinate phænomena in the chain of causation from the great First Cause.

The brief record of creation in the Sacred volume leaves us to infer that certain plastic and spermatic qualities of

common matter were operative in the production of the first organized Beings of this planet. "The earth brought forth grass and herb yielding seed after his kind, and the tree yielding fruit whose seed is in itself." "The waters brought forth abundantly the moving creature that hath life;" and "the earth brought forth the living creature after his kind, cattle, and creeping thing, and beast of the earth." But of our own species it is written, "God created man after his own image, in the image of God created he him; male and female created he them." And "God said unto them, Be fruitful, and multiply and replenish the earth." (Gen. i. 27 and 28.)

Since that first fiat went forth, the propagation of the species of plants, animals and mankind has been left to the operation of certain natural secondary causes, which we sum up as the 'act of generation.'

Botanists and physiologists have observed and progressively analysed the phænomena until they have reduced them to a great degree of simplicity, the essential conditions being the same, or closely similar, in both realms of organic nature.

With regard to the animal kingdom, the generation of which here concerns us, the essential conditions of the act appear to be a nucleated cell, and the product of a nucleated cell, with the combination of the two: the nucleated cell is the 'germinal vesicle,' and is the essential part of the ovum; the other nucleated cell is the 'sperm-cell,' and its product is the spermatozoon.

It is essential to the development of the germ that the ovum receive the matter of the spermatozoon: it is then said to be impregnated.

The phænomena that thence ensue are essentially the same up to a certain point in all animals, and consist in the formation of a germ-cell (Pl. I. fig. 4, *c*), and its propagation of a numerous offspring (fig. 10) at the cost of the germ-yelk (fig. 4, *a*), by a series of reiterated spontaneous

divisions. The right and clear comprehension of the purpose of this process, or the object effected by it, is essential to the elucidation of the nature and relations of the subsequent modifications and varieties in the course of development. The progeny of the 'primary impregnated germ-cell' may be called 'secondary' or 'derivative impregnated germ-cells,' and the whole is the 'germ-mass.'

The progeny of the impregnated germ-cell resemble their parent, with a diminution of size, to a certain stage of descent, when they may be ultimately reduced to their essential parts or nuclei (fig. 11). When they cease to exist as germ-cells or nuclei of such, either by coalescing with others or by liquefaction, they do not lose their vitality: as individuals, indeed, they may be said to die, but by their death they minister to the life of a being higher than themselves (*e. g.* figs. 12, 13). They combine to construct its tissues or dissolve and impart properties to its fluids; these metamorphoses being mysteriously governed by a plastic nature or mode of force operating unconsciously upon the matter, but according to a law of order and harmony, and to a fore-ordained and definite end, resulting in a distinct and specific form of animal adapted by its organization for a particular sphere of existence, and forming a more or less valuable, but not, as once was thought, an essential link in the great chain of organic life.

Not all the progeny of the primary impregnated germ-cell are required for the formation of the body in all animals: certain of the derivative germ-cells may remain unchanged and become included in that body which has been composed of their metamorphosed and diversely combined or confluent brethren: so included, any derivative germ-cell or the nucleus of such may commence and repeat the same processes of growth by imbibition, and of propagation by spontaneous fission, as those to which itself owed its origin; followed by metamorphoses and combinations of the germ-

masses so produced, which concur to the development of another individual; and this may be, or may not be, like that individual in which the secondary germ-cell or germ-mass was included.

It has been found that in proportion as the subjects of anatomical investigation descend in the scale of animal life, the number of the derivative germ-cells and nuclei which retain their individuality and spermatic power is greater, and the number of those that are metamorphosed into tissues and organs less.

Cells predominate in the tissues of the vegetable kingdom, the lower members of which consist exclusively of them, and have been thence called 'plantæ cellulares:' the lowest of all consist of a single nucleated cell.

The animal kingdom starts from the same elementary beginning: a cell-wall forms the smooth elastic and contractile integument of the *Gregarina**: a fluid with granules, and a firm nucleus which sometimes contains one or more nucleoli,—the ordinary cell-contents,—are the sole representatives of organs or viscera. Yet the power of the *Gregarinæ* to live and grow independently by assimilating foreign nutriment, the vital contractility of their tegumentary tunic, their chemical composition and their definite forms, with such well-marked specific characters, in a few instances, as the *Greg. brevirostris* and *Greg. Sieboldii* present, render their interpretation by Kölliker as a low and primitive form of parasitic animal, the most accordant with actual physiological and zoological knowledge†.

The Gregarina is a single-celled animal, which differs from the single-celled plant by the vital contractility of its tissue, and the solubility of its cell-wall in acetic acid. Devoid of mouth, stomach, or any other organ properly so

* A genus of microscopic parasites which infest gregariously the internal cavities and canals of insects and worms.

† Kölliker, 'Ueber die Gattung *Gregarina*,' Zeitschrift für Wissenschaftliche Zoologie, Bd. i. p. 10, 1848.

called, it reduces our definition of an animal to the difference indicated in the preceding comparison.

The Polygastric Infusoria exhibit the next step in the progress of individualizing a higher independent embodiment of animal life. A firm central nucleus in which, as in the Gregarina, resides the self-repellent property of spontaneous division, indicates, however, their essential character as animated cells. But the granular contents have been developed into secondary cells; and some of these have combined and coalesced to form special organs, such as cavities for digestion, pulsatile cells for circulating a clear plasmatic fluid, an irritable and contractile integument beset with vibratile cilia: yet a large proportion of the contents of this modified primary cell-wall consists of unchanged secondary cells.

In the freshwater polype, *Hydra*, an external layer of cells is partially condensed into an integument, and an internal layer modified to form the gastric secerning villi: in the tentacula a greater proportion of the derivative cells have been metamorphosed into the muscular bands, the nodosities, the prehensile darts and tactile cilia. But the chief point that I have now in view is to draw attention to the large proportion of retained and unaltered nucleated cells and nuclei, which are identical in all recognizable characters with the progeny of the primary impregnated germ-cell, and which are ready, therefore, when favourable circumstances concur, to repeat the acts of assimilation and spontaneous fission, and, each individually, thus to lay the basis of a new polype.

A large proportion of the derivative germ-cells is retained unchanged in the compound hydriform polypes and in the parenchymatous Entozoa: a smaller proportion in the Acalephæ and cavitary Entozoa. Derivative germ-cells are aggregated in the last segment of the Nais, and of the young of other Annelides. We find derivative germ-cells, and masses of nuclei like those resulting from

the final subdivision of germ-cells, retained unchanged at the filamentary extremities of the branched uterus forming the ovaria of the larval Aphides.

In most of the lower classes of animals the course of development is temporarily arrested at certain stages, though growth may go on; the embryo moving and feeding, and perhaps propagating, as if it were a completed individual, usually under a form very different from that which itself or its progeny are destined ultimately to assume; whence these arrested forms have been termed 'Larvæ,' the true lineaments of the fully developed form being hidden, as it were, beneath a mask.

The earlier the individual in any of these larval stages may have been arrested from the commencement of its development from the germ-mass, the greater is the proportion of the derivative impregnated germ-cells and nuclei that continue unchanged in its constitution: and the result of the retention of these, in the hydriform larvæ of Acalephes, *e. g.*, is the exercise, as in the mature freshwater Hydra, by one or more of such retained progeny of the primary impregnated germ-cell, of the powers derived from the legacy of the portion of the spermatic virtue which they received from their parent nucleated cell.

In the Polygastria, *e. g.* when favourable influences of warmth, light and abundant nutriment concur, a central body, which represents the nucleus of the impregnated germ-cell, sets on foot the special act of assimilation and spontaneous fission; and its divisions seem to repel each other to positions equidistant from each other, and from the pole or end of the body to which they are nearest.

The influence of these distinct centres of assimilation is to divert the flow of the plasmatic fluid from a common course through the body of the Polygastrian to two special courses about those centres. So much of the primary developmental processes is renewed, as leads to the insulation of the sphere of the influence of each assimilative centre

from that of the other by the progressive formation of a double party-wall of integument, attended by progressive separation of one party-wall from the other, and by concomitant constriction of the body of the Polygastrian, until the vibratile action of the superficial cilia of each separating moiety severs the narrowed neck of union, and they become two distinct individuals. An eye-speck, a pulsatile sac, a proboscis, or whatever organ may be required to complete the specific characters of the particular Polygastrian, are likewise developed, and the individualization of each moiety is thus completed.

This mode of propagation is termed 'spontaneous fission.'

In the freshwater polype the progeny of the primary impregnated germ-cell retained unaltered in the body, may set up, under favourable stimuli of light, heat and nutriment, the same actions as those to which they owed their own origin: certain of the nucleated cells do set up such actions, those, *e. g.*, in the *Hydra fusca*, which are aggregated near the adhering pedicle or foot; and the result of their increase by assimilation and multiplication is to push out the contiguous integument in the form of a bud, which becomes the seat of the subsequent processes of growth and development: a clear cavity or centre of assimilation is first formed, which soon opens into the stomach of the parent: but the communication is afterwards closed, and the young Hydra is ultimately cast off from the surface of the parent.

This mode of propagation is termed 'Gemmation.' It differs from the development of the Hydra *ab ovo* inasmuch as the impregnated germ-cell, which set on foot the process, is derivative and included in the body of the adult, instead of being primary and included in a free ovum. But the germ-cell is the essential part of the ovum, and the chorion an accessory and non-essential part.

The very small size in relation to the entire body, and the superficial position, of the derivative germ-cell which takes

on the processes of development in the Hydra, appear to be the chief conditions influencing that modification of the generative process by which a small portion only of the Hydra is taken into the system of the new individual, instead of one-half of the body, as in the case of the Monad. So insignificant is the distinction between gemmation and spontaneous fission; the essential condition of both being, as in the development of the ovum, the presence of the pellucid nucleus of a derivative germ-cell, as the centre from which all the processes in the formation of the new individual radiate.

The Hydra propagates by ova as well as by buds. Certain of the retained fertile germ-cells multiply themselves, and coalesce to form a larger central cell, surrounded by others of the ordinary smaller size, the exterior of which are metamorphosed into a chorion. Certain other germ-cells are converted into sperm-cells, and develope spermatozoa. The ova are extruded and fertilized by these: each constitutes the first term of a new series of life and developes a Hydra, which retains however a large proportion of unchanged cells in its composition. Accordingly this Hydra may propagate by buds, and the Hydra so developed may propagate again by ova, and these two kinds of generation may alternate indefinitely.

In most of the marine hydriform polypes, the delicate tissue of the body is supported in the waves and breakers, and protected from the briny element by an external horny integument. Were such a polype to propagate by gemmation, and the external crust to grow with the growth of the bud, and expand to protect the soft digestive sac of the new polype, an apparently compound animal would result from the number of individuals so held together. Such is the nature of a vast family of marine zoophytes which our Lyncean Ellis has so accurately described and beautifully figured as 'Corallines*,' and which are grouped

* An Essay towards a Natural History of Corallines, &c., 4to. 1755.

together in modern systems of zoophytology under the name of 'Hydrozoa*' or Anthozoa Hydroidea†.

These also must propagate by ova, in order that the species may be dispersed. In some species the germ-cells are metamorphosed into ova at particular parts, and the concomitant growth of the soft tissue and outer crust furnishes those ova with a capsule (Pl. I. fig. 2, *f*); which modification in the growth of the coralline Prof. E. Forbes compares with that "metamorphosis in flowering plants in which the floral bud is constituted through the contraction of the axis and the whorling of the individuals borne on that axis, and by their transformation into the several parts of the flower."

The ova may escape from the ovi-capsule in the condition of ciliated locomotive bodies, called 'planulæ' by Sir John Graham Dalyell; or the planulæ may be hatched in the interior of a polype-individual developed from the summit of the ovi-capsule, and which, after liberating them, may wither and fall like the flower of a plant, as in some *Campanulariæ* ‡. Or a generative individual of a particular form § may be developed and become detached, and, by its own power of locomotion, carry the contained ova to a distance from the composite and fixed group of nutritive individuals.

The ova may be developed within the bell-shaped Acalephoid prior to its detachment, as in the *Coryne vulgaris*, observed by Wagner ||, or not until it has become de-

* Owen, Lectures on the Comp. Anat. and Physiology of the Invertebrata, p. 82, 8vo, 1843.

† Johnston, History of British Zoophytes, p. 5, 8vo, 1846.

‡ Lister, Phil. Trans. 1834, p. 375, pl. 10. fig. 1, 5, 6. (See Pl. I. fig. 2, *g*, *i*.)

§ *E. g.* the *Medusa octocilia* and *duodocilia* of Dalyell, from *Eudendrium ramosum*; and the *Tintinnabulum* or Bell-medusa (Pl. I. fig. 2, *l*) observed by the same author to be developed from the *Campanularia dichotoma*.—Edinb. New Philosophical Journal, vol. xxi. 1836, p. 91.

|| Isis, 1833, p. 256, t. xi.

tached and acquired the full characters of a bare-eyed Medusa*

This remarkable phænomenon is best shown in the claviform Corallines, and has been especially described by Lovèn† in an excellent memoir on the *Syncoryne ramosa*, and by Steenstrup in the *Coryne Fritillaria*‡. This species originally developes a many-armed digestive polype or individual, which retains a large proportion of unchanged germ-cells: these, by the stimulus of the excess of nutriment, begin to repeat the process, and push out buds in an analogous position to that in the *Hydra fusca*, viz. around the base of the stomach of the first or parent animal: but the buds, instead of repeating the form and condition of that animal, take on a higher form, resembling that of a bell-shaped Medusa; they become detached and swim off to a distance, forming and discharging the ova, which, as Steenstrup conjectures, in their turn develope the fixed polype-shaped *Coryne*.

This stage of the cycle has not yet been the subject of observation; but, by the analogy of the larger Medusæ, is the more probable process than that direct metamorphosis of the medusiform individual into the pedunculate polypoid individual, which V. Beneden has described by the aid of a conjectural figure in the *Tubularia* §.

The medusiform ovigerous locomotive or distributive individual of the *Coryne* and *Campanularia dichotoma* is obviously homologous with the polypiform ovigerous individual, which seems to nurse, as it were, the ova into 'planulæ' in the *Campanularia geniculata*; and the nutritive gemmiparous polypiform individuals in all the com-

* See the beautiful and philosophically treated monograph on the *Gymnophthalmata*, by Prof. Edw. Forbes; published by the Ray Society. 4to, 1848.

† Wiegmann's Archiv für Naturgeschichte, 1837, p. 322, t. vi.

‡ 'On the Alternation of Generations,' translation by Ray Society, 8vo, 1845, p. 26, pl. 1. figs. 41–45.

§ Recherches sur l'embryogénie des Tubulaires, 4to, 1844, pl. 2. fig. 5.

pound Radiaries would seem, rather than the oviparous medusiform ones, to manifest the typical form of the species; as the leaf is a more typical form of the plant than the parts of the flower; and as the free-swimming Cirripedal larva, with its pedunculated eyes, is more typical of its class than is the blind and fettered multivalve Barnacle into which it is so marvellously transformed. Superadd, however, distinct nutritive and circulating organs to the free-moving ovigerous individual from the rooted polype, and prolong its existence, and it would then cease to have the ancillary character of a nurse to the ova of the fixed individuals, and would assume that of the perfected form of the species, and such in fact is the case with the larger gelatinous Radiaries called *Medusæ*.

The egg of the species called *Cyanæa aurita* is devoid of a chorion*, and consists, after impregnation, of the germ-mass only, formed according to the before-defined process for the dissemination of the spermatic principle †. By the combination and metamorphosis of the peripheral series of secondary germ-cells a ciliated epithelium is formed ‡: an assimilative cavity § results from the liquefaction of certain central germ-cells: the germ-mass grows, elongates, and is

* Siebold, Beiträge zur Naturgeschichte der Wirbellosen Thiere, 4to, 1839, p. 21.

† The external signs of these universal preliminary steps in development *ab ovo* are figured in the above-cited work, in tab. 1. figs. 1–13. The preliminary internal changes may be inferred from what was observed by Siebold and Bagge in the ova of the *Strongylus auricularis* (*De Evolutione Strongyli*, 4to, 1841), some of whose figures are copied in my 'Lectures on the Invertebrata,' 8vo, 1843, p. 77, figs. 33–44, where I remark, as Dr. Martin Barry had, also, independently remarked (see the note which he communicated to the same work) :—"This preliminary division of the clear central cell to the spontaneous fission of the yelk is closely analogous to that division of the central cell in the polygastrian animalcule, preparatory to the spontaneous division of its body into two individuals, which Ehrenberg described." (See Pl. I. figs. 4—13 of the present 'Discourse.')

‡ Siebold, *loc. cit.* fig. 19. § Ib. fig. 15.

thus metamorphosed into an animal, which, like the 'planula' of the Hydrozoa, typifies the ciliated infusorial *Leucophrys*; ciliated lobes, like those of a Rotifer, are next developed from one extremity; these grow into arms, and the whole animal assumes the form of a polype: as such it was originally described by Sir J. G. Dalyell, under the name of *Hydra Tuba*, and in this state it propagates by gemmation.

The condition of this 'Parthenogenesis,' or power of propagation by the virgin larval polype, appears to reside, as in the *Hydra fusca*, in the following structure: "The body and tentacula of the larva are composed of two distinct layers, an internal and external. The internal layer chiefly consists of nuclei and nucleated cells of various sizes, some of them containing a large number of nuclei; while the external is chiefly composed of a structureless substance with numerous minute nuclei disseminated through it*." Sir J. G. Dalyell obtained a colony of eighty-three *Hydræ Tubæ*, by buds, from one parent. But the procreative force is not hereby exhausted. After one, two or more years of captivity the body of the polype has been observed to become thickened and impressed by circular grooves: these, deepening, divide the outer surface into rings, and this annulated part of the body may be supported on a contracted and smooth base; the whole polype being lengthened by the successive development of the segments so indicated: the margins of these segments next shoot out short tentacles in eight pairs, and then the whole of the annular part† is resolved by a series of spontaneous fissions into as many small medusiform discs, which by growth and a minor amount of metamorphosis are developed into true Medusæ. In certain of these individuals sperm-sacs

* Dr. J. Reid's 'Observations on the Development of the Medusæ.'—Taylor's Annals of Natural History, 1848, p. 26.

† The base may remain, reproduce the arms of the Hydra, and again propagate by gemmation and spontaneous fission.

and spermatozoa are developed; in others, ovisacs and ova: thus distinct males and females are produced, combining the nutritive with the generative functions. The ova are impregnated, are sheltered for a time in special marsupial pouches, the parent also performing the part of a nurse, and then the young brood issues forth under its ciliated or infusorial form. From the polygastric type it passes into the rotiferous one, from this into the polype type, and all the individuals propagated by gemmation under the latter form are ultimately resolved by spontaneous fission into the male or female oviparous Medusæ.

I will cite a few other instances in which a species is represented by a series of individuals of different powers and forms succeeding each other in a cycle. Certain fresh-water snails are infested by Entozoa of the order *Trematoda* or fluke-worms; as the *Limnæa stagnalis e. g.* by the *Distoma tarda.* The ova, or products of the ova, of this species are found, in early summer, adhering in vast numbers to the inner surface of the respiratory cavity and to the exterior of the lobes of the liver and generative organs of the snail; where they increase in size, and detach themselves as free animalcules, assuming a bright yellow colour, whence they were called by Bojanus "konigsgelben Würmern," and manifesting a twisting vermicular motion. If one of these be microscopically examined, none of the lineaments of the organs of the future *Distoma* can be discerned; they resemble in structure rather the *Gregarinæ,* consisting in fact of little else than the germ-mass, a small proportion of which may have been metamorphosed to form the smooth outer skin.

As the growth of this Gregariniform parasite proceeds, a progeny is seen to rise in its interior by the aggregation round separate pellucid centres of the nuclear matter into numerous independent germ-masses, and their development into embryos: these are first manifested by the appearance of an anterior and a median circular sucker, and then they acquire cephalic spicula and a

vibratile caudal appendage: they escape from the parent cyst, bore their way out of the snail, and disperse themselves as free swimming ciliated Cercariform animalcules in the water. After a brief enjoyment of this free and active state of existence, they shrink in size, the vibratile tail is cast off, and they attach themselves to the skin of the snail. Here they become buried, form for themselves a pupa-case out of the condensed mucus, and are metamorphosed into true *Distomata*, which gain their parasitic habitat by piercing the soft integument of the water-snail. Thus we have a Trematode entozoon successively assuming the form of a *Gregarina*, a *Cercaria*, and a *Distoma*; one impregnated ovum developing many individuals of the second form, each of which finally passes into the third form*.

But this does not give the entire metagenetic cycle of the Entozoon. The gregariniform parent of the cercarial larvæ is most probably the product of the ovum of the *Distoma tarda*, not the ovum itself, the development of which, in this species, has not yet been seen. From the analogy of those *Trematoda* in which that development has been traced, *e. g. Monostoma mutabile*, *Distoma tereticolle*, *Dist. hians*†, *Dist. hepaticum*, *Dist. cylindraceum*, *Dist. globiporum*‡, *Dist. duplicatum*, *Dist. longicolle* and *Amphistoma subclavata*, the first product of the ovum is a free-swimming ciliated animalcule, and so like a polygastric infusory as to have been described as a *Paramæcium*. Siebold, to whom we owe the most precise and valuable information of this first link in the chain of self-active individuals, found that this animalcule was hatched in the oviduct of the *Monostoma mutabile*, was excluded from the egg by pushing off its opercular cap, and then escaped from the vulva. The ciliated integument inclosed a fluid

* Steenstrup, *op. cit.* p. 52, pl. 3. Siebold, Archiv für Naturgeschichte, 1843, p. 321.

† Mehlis, Oken's Isis, 1831, p. 190.

‡ Nordmann, Mikrographische Beiträge, Heft 2. p. 139.

with fine granules, and a subcentral colourless, transparent structureless body, which, if the whole animalcule were compared to a ciliated single-celled animal, would stand in the relation of a nucleus to such cell. But this nucleus has a very definite form: it is elongated, pointed at one end, obtuse at the other end, on each side of which stands out a short thick process. The ciliated integument of the animalcule, after a brief course, ruptures, decomposes, and sets free the body we have compared to the nucleus. This body then increases in size, manifests a smooth non-ciliated skin, and begins to show an extremely fine granular structure, but no other organ. Siebold, however, who could not but recognize it as an independent individual organism, asks if it might be a parasite of the infusorial-like embryo of the Monostoma, but observes that the constancy of its existence in such was opposed to that idea, and he points out its resemblance to the parents of certain *Cercariæ* described by Bojanus and V. Baer. The solitary progeny of the ciliated embryo of the trematode Entozoon is closely similar in form and structure to those gregariniform animalcules, since described and figured by Steenstrup*, in which are developed the numerous cercariform individuals that he saw ultimately metamorphosed into trematode Entozoa.

The testimony of different good and independent witnesses at different periods to different stages of the successive generations, which, when compared with one another, are seen to link together and complete the metagenetic cycle, is perhaps the best foundation for scientific confidence in the truly marvellous result.

Siebold† observes the development and birth of the ciliated monadiform embryo from the egg of the viviparous trematode Entozoon, and the escape of the gregariniform non-ciliated worm from the ciliated one.

* 'On the Alternation of Generations,' Ray Society's Translation, 8vo, 1845, tab. 2. figs. 2 *a—d*.

† Wiegmann's Archiv für Naturgeschichte, 1835, Bd. i. p. 67.

Bojanus* and V. Baer† trace the development of the cercariform individuals from the 'king's-yellow worm,' which in its form and simple structure corresponds with the vermiform offspring of the first ciliated embryo.

Nitzsch‡ traces the cercariform progeny of that worm to their pupa state.

Steenstrup§, confirming the origin of the Cercariæ from the multiparous 'king's-yellow worm,' completes the observation of their metamorphosis through the pupa-state into the trematode Entozoon.

The conditions of structure to be considered in the attempt to explain the successive parthenogeneses are the following.

In the *Distoma tereticolle*‖ the first germ-cell, which is the result of impregnation, multiplies itself in the usual geometrical ratio, progressively absorbing and assimilating the germ-yelk, until a germ-mass of countless minute cells is formed; but the subdivision and diffusion of the spermatic force is carried further by the reduction of the progeny of the primary germ-cell to the size and apparent state of nuclei or granules; in which state, with a clammy fluid vehicle, inclosed in a vermiform sac, usually composed of a ciliated integument and sometimes provided with one or more eye-specks, the germ-mass quits the ovum. We perceive, therefore, that it has undergone no other change than that which has contributed to the formation of such peripheral parts. There are no proper internal organs. In the *Monostoma mutabile* it would seem that the true nuclear matter of the germ-cells had, after their ultimate subdivision, aggregated itself together in the centre of the ciliated embryo or modified germ-mass. In that aggregated

* Isis von Oken, 1818, p. 729.

† Beiträge zur Kenntniss der Niederen Thiere, Nova Acta Leop. Car. tom. xiii. pt. ii. p. 629.

‡ Beitrag zur Infusorienkunde, Halle, 1817.

§ On the Alternation of Generations, p. 52.

‖ Kölliker, Müller's Archiv für Physiologie, 1843, p. 99.

state it is liberated from the locomotive germ-mass; but with the exception of a smooth peripheral extensible integument which now invests it, the nuclear matter has exhausted no force in the formation of organs. The nuclear particles begin first to operate, apparently by self-repulsion, thus making themselves discernible; and by the attraction and assimilation of the foreign organic matter of the animal which the ciliated parent may have penetrated, a certain growth ensues; the nuclear contents then resolve themselves into numerous distinct germ-masses. These are in a great degree metamorphosed into the organs of as many Cercariæ: the unused-up cells, with the remnant of the spermatic force, are exhausted in converting each Cercaria into an androgynous Entozoon. In this final form the spermatic force is mysteriously renewed in the appropriate male organ; ova are simultaneously prepared for its reception, after which its dissemination recommences by the formation of the germ-mass in each impregnated ovum.

Here, amongst other topics suggested by the phænomena just described, we may ask, whether all the *animæ*, or manifestations of self-perceptivity and self-activity, of the several 'Paramæcioids,' 'king's-yellow worms,' 'Cercariæ' and 'Trematoda,' pre-existed as independent principles in the single impregnated ovum from which those animals are to proceed. And we might enter upon the interesting and important inquiry how, and how far, these phænomena of Parthenogenesis may determine the long-mooted question of the relation of such vital principles or manifestations to the organization of the individual. But this is foreign to my present object, if even time permitted, and I proceed therefore to the other instances of cyclical generation.

V. Baer, who led the way in experimenting and observing the artificially impregnated eggs of the Sea-urchin (*Echinus*), found them to be first developed into a ciliated monadiform animalcule, like that of the *Medusa aurita*.

In the course of four days this animalcule had become metamorphosed into (or had given birth to?) a minute transparent acalephoid creature which he compares to a Beroë. Here his observations ceased, the animals having perished on the fifth day.

In the autumn of 1845 Prof. Müller had discovered in the sea at Heligoland a transparent acalephoid animalcule, referable by its mode of motion to the 'ciliograde' order, but which, from its singular form, somewhat resembling a painter's easel, he described under the name of *Pluteus paradoxus**.

Returning in the following year to the same field of observation, he pursued with admirable detail the change of this species into an *Ophiura* (Brittle star-fish), and that of another kind of Pluteus into an *Echinus*†.

The larva of the Echinus, like that of the Ophiura, has a quadrilateral pyramidal body, of a colourless, transparent, or hyaline substance, dome-shaped above, slightly excavated at the base, the corners of which are prolonged into straight slender legs, strengthened by filiform rods of calcareous matter, reaching to the summit of the dome: the mouth is prolonged from the middle of the concave base into a four-sided proboscis, the angles of which are also produced into slender processes shorter than the four outer legs. Were the creature to stand upon these it would resemble a table-clock case, and the proboscidiform mouth and appendages might swing to and fro like the pendulum. The larva is, however, a free-swimming animalcule, and propels itself, with the base and processes forwards, chiefly by means of strong cilia, grouped on two tubercles at the sides of the dome, which are compared to epaulets. In the centre of the dome-shaped body is a subspherical granular mass, which

* Archiv fur Anat. und Physiol. 1846, p. 101.

† 'Ueber die Larven und die Metamorphose der Ophiuren und Seeigel,' Vorgetragen in der Kön. Akad. der Wissenschaften, 29 October 1846; 4to, 1848.

Prof. Müller calls the stomach, and which doubtless surrounds the cavity to which the mouth and pharynx conduct.

The first evidence of the change to the Echinus is the formation of a circular disc, like a clock-face, on one side of the granular mass: five double lines, like pointers, radiate from the centre of this disc, and their extremities expand into circles with a double outline. These circles form the bases of as many hollow tentacles, like those that traverse the ambulacral pores of the adult Echinus, but which are here single, not in pairs. Triradiate pedicellariæ appear, two on each side the disc, of the kind called 'gemmiform' in the adult Echinus. The disc progressively expands, extending over the cellular mass to which it owes its origin, and developes tubercles, which push through the transparent dome of the Pluteus, and are transformed into spines and tentacles, both of which, together with the pedicellariæ, manifest their characteristic motions and combine these seemingly voluntary actions with the automatic continued vibrations of the ciliated epaulets of the larva; so that it can now both swim and creep. By the time the disc has grown over half the granular sphere little of the larva remains, except some of the slender calcareous rods: the perforated oviducal plates of the nascent Echinus are formed round the pentagonal space, as yet imperforate, in the centre of the original disc, determining the anal pole of the developing spiny globe, close to which the cicatrix of the ruptured pharynx of the Pluteus is completed by the so-called 'madreporiform plate.' The mouth of the Echinus is quite distinct and remote from that of the Pluteus, and is first indicated in the centre of the naked or unspined moiety of the granular sphere by the formation of the hard summits of the five characteristic jaws and teeth of the Echinus. The outer skeleton is completed by the progressive extension of the 'ambulacral' and 'interambulacral,' or spine-bearing plates, and by the less regular 'oral' plates.

Thus the Echinus is fully manifested, and becomes either

a male by the development of testes, or a female by that of ovaria. The ova are impregnated, and develope the monadiform embryo; this gives origin to the beroiform Pluteus, which produces by 'metagenesis,' rather than by metamorphosis, the young Echinus, and the cycle is completed by its growth into the oviparous adult.

Passing to another great group of Invertebrate animals, the Mollusca, we learn from the observations of M. Milne-Edwards*, Dalyell† and Sars‡, that the embryo developed from the ovum of the compound Ascidiæ quits the receptacle of the fixed parent in the form of a large Cercaria, *i.e.* with a caudate appendage, as a freely swimming animalcule; then finally settles, becomes attached to some foreign body, developes the organization of the Ascidian, and propagates by gemmation the compound group of such Mollusca, which in their turn develope ova producing freely-swimming tadpole-like larvæ.

Chamisso was long ago led by his observations during Kotzebue's circumnavigatory Voyage to the conclusion, that the solitary Salpæ gave birth to embryo Salpæ of a different form, and connected together in chains; from each individual or link of which a solitary embryo is produced, which grows and assumes the characters of that Salpa from which the chain of embryo Salpæ again proceeds.

The Nais and the young of many marine Annelides propagate by gemmation from the terminal segment of the body a succession of other individuals like themselves, and the characteristics of the head of the parent, whether a proboscis or eye-specks, antennæ or branchiæ, are recognisably developed upon the anterior segment of the still attached offspring. Before this is cast off, the gemmiparous segment of the parent repeats its procreative office, and a

* 'Observations sur les Ascidies Composées,' 1841.

† Edinb. New Philosophical Journal, 1839.

‡ Cited by Steenstrup, *op. cit.* p. 48.

second young annelide is formed: sometimes a third, a fourth, a fifth, and even a sixth may be generated, and thus seven individuals may be seen organically connected in a linear series*. They are ultimately separated by spontaneous fission. The gemmiparous parent has no generative organs: these are developed in its offspring, which propagate by impregnated ova, producing in the Nereids a ciliated monadiform embryo, metamorphosed into the setigerous worm, which produces by gemmation and spontaneous fission the true males and females of its species†.

Closely analogous to this alternating mode of reproduction, and to that cyclical succession of differently formed individuals which has been adduced from the Medusa and the Distoma, are the generative phænomena presented by certain members of the class of Insects, in which many individuals are the product of a single impregnated ovum, and are produced in successive generations from the individual proceeding from that ovum.

It is now more than a century since Bonnet‡ first attracted the attention of physiologists and naturalists to this mode of generation in the *Aphides* or Plant-lice. And because it was the first of a large class of phænomena, till then utterly unknown and unsuspected, it was received with considerable doubt, or met by total incredulity.

The facts are briefly these.

The impregnated ova of the Aphis are deposited, at the close of summer, in the axils of the leaves either of the plant infested by the species or of some neighbouring plant, and the ova retaining their latent life through the winter, are hatched by the returning warmth of spring: a wingless hexapod larva is the result of the development. This larva, if circumstances, such as warmth and food, be favourable, will produce a brood, and indeed a

* Milne-Edwards, 'Annales des Sciences,' 1845, pl. 11. fig. 65.

† Ibid. p. 170.

‡ 'Traité d'Insectologie, ou Observations sur les Pucerons,' 8vo, 1745.

succession of broods, of eight larvæ, like itself, without any connection with the male. In fact no winged males at this season have appeared. If the virgin progeny be also kept from any access to the male, each will again produce a brood of the same number of aphides: and carefully prosecuted experiments have shown that this procreation from a virgin mother will continue to the seventh, the ninth, or the eleventh generation before the spermatic virtue of the ancestral coitus has been exhausted.

When it is so exhausted, a greater proportion of the nuclear germ-masses retained by the last procreant larvæ is used up: individual growth and development proceed further than in the parent: some members of the last larval brood are metamorphosed into winged males, others into oviparous females. By these the ova are developed, impregnated and oviposited, and thus provision is made for disseminating the individuals and for continuing the existence of the species over the severe famine-months of winter.

The metamorphosis in all insects is attended with the casting off or creeping out of a certain proportion of the precedent individual, which process is called the 'ecdysis' or moult. With regard to the so-called metamorphoses which issue in the succession of a fixed, blind, sessile multivalve barnacle to a free-swimming crustacean with pedunculated eyes*, or in the succession of a rooted vermiform parasite to a natatory animal with articulated setigerous limbs†—when these phænomena are closely traced, they are seen to depend in a greater degree upon the action and coalescence of retained cells, than upon a change of pre-existing tissues. If the development of the ovum in the pedunculate ovarian sac of the low organized crustaceous epizoon of a fish be closely traced, the peripheral cells of the germ-mass are seen to combine and coalesce to form the smooth transparent skin of the

* J. V. Thompson, Zoological Researches, 8vo, p. 69.

† Nordmann, Mikrographische Beiträge, Heft ii. 1832.

embryo Lernæa, from which also tubular processes extend in two (*Achtheres*) or three (*Lernæocera*) pairs, including setæ which project from their extremities.

In the *Lernæocera* the anterior pair is directed forward like antennæ, but they are unjointed; and the head is further indicated by a coloured eye-speck. Another layer of germ-cells has perished, as such, in order to form the parietes of a straight and simple intestine, with a mouth and anus. Thus the annelidous type is first manifested.

But a large proportion of the minute germ-cells remain in the wide abdominal interspace, amassed around the alimentary tube, and aggregated in groups at the base of the tubular and setigerous feet. With respect to the latter we might say that the same provision is made for the reproduction of the limbs as is retained throughout life in regard to those of the Lobster. In the larval Lernæa, however, those reserve-cells commence the formation of new limbs irrespective of any injury to the old ones. The whole peripheral stratum of the retained germ-mass in contact with the primary integument is transformed into a new integument. These germ-cells have increased and propagated at the expense of the aliment assimilated by the alimentary canal. The formation of the new integument and of the new feet proceeds connectedly and contemporaneously: but the new parts are not moulded upon the inner surface of the old ones. The plastic force has changed its course of operation. A hinder segment of the body is added to the front one which answers to the whole of the body of the first larva. If antennæ did not before exist, a jointed pair is now developed. Instead of two pairs of tubular setigerous limbs, three pairs of uncinated prehensile limbs are developed from the anterior or cephalothoracic segment, and as many pairs of articulated setigerous limbs from the abdominal segment. New muscles, new nerves, and new vessels are formed for the support and exercise of these various instruments. The outer

case, and all that gave form and character to the precedent individual, perish and are cast off: they are not changed into the corresponding parts of the new individual. These are due to a new and distinct developmental process; rendered possible through the retention of a certain proportion of the unchanged germ-cells and nuclei. The process is essentially the same as that which developes the cercariform larva of the Distoma within the gregariniform one, or the external bud from the Hydra, or the internal bud from the Aphis. It is a slightly modified parthenogenesis: and the phases by which the locomotive annelidous larva of the Lernæa passes through the entomostracous stage before retrograding to the final condition of the oviparous, limbless, bloated and rooted parasite, are much more those of a metagenesis than a metamorphosis.

The instances which I have adduced are a few out of many that have been truly observed and faithfully recorded by zealous and acute men who have devoted themselves to the observant service of Nature, in hope of reward by an insight into her secret operations for the multiplication of the species of the lower invertebrated classes of animals. These observations have already demonstrated the generation of many individuals from a single impregnated ovum to be, in those classes, the rule and not the exception: they have shown that the mode of that manifold generation is similar in its essentials, though diverse in its accessory circumstances, as in all other acts and things in Nature. Bonnet, Chamisso, Von Baer, Ehrenberg, Dalyell, Milne-Edwards, Sars, Lovèn, Siebold, Lister, Steenstrup, Müller, Kölliker and others have enriched their science with valuable stores of such facts; and they have mutually corrected or confirmed the impressions derived from the observation of the remarkable phænomena. These phænomena remain, however, at present on record as such simply: they have been generalized as being dependent on a law*:

* By Steenstrup, in the Essay above cited.

but this law, or the condition essential to their occurrence, has not, so far as I can learn, been recognized. I arrived, however, some years ago*, at what I felt to be a clear insight into the circumstances which rendered the successive generations from virgin Aphides possible and conceivable, and I have the greater confidence in the truth of that insight from finding it equally explanatory of the analogous phænomena of 'Lucina sine concubitu' in other animals.

These phænomena, first observed, as I have said, by Bonnet, in the genus *Aphis*, were the first to which the thoughts of physiologists were bent to explain. But being viewed in the light of a strange and anomalous exception, and at a period when the phænomena of embryonic development were not known, the earliest steps more especially, success could not be expected.

Reaumur eluded the difficulty of the fact which Bonnet had discovered, by affirming the Aphides to be androgynous. The vagina in the perfect oviparous females has appendages called spermatheca and colleterium: and Reaumur might have even appealed to the microscope in support of his idea, for he would have detected, by its aid, spermatozoa in the spermatheca. But this would not have proved the hermaphroditic structure; for the spermatheca receives the intromittent organ of the male, and retains the semen in store for the successive impregnation of the ova as they pass out: the ova at the same time being coated by the adhesive and protective matter of the colleterium. These appendages of the vagina are found in most oviparous insects: and the true male Aphis is as well known now as that of any other species of Insect. Moreover, it is found that the viviparous virgin larvæ of the Aphides have not got a trace of those appendages of the vagina, which Reaumur supposed to be male organs. They were not required in her mode of generation and are not developed: the germ-

* Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals; 8vo, 1843, pp. 234, 366.

cell already exists in her with sufficient spermatic and plastic force for its development: no semen, therefore, needed to be retained, and there is no spermatheca: the embryonic development is completed *in utero*, and no secretion for the protective covering of ova was needed. The structures therefore which Reaumur, under a misconception of their nature, cited in order to solve the problem of the alleged virgin procreation, are present only in that perfect form of Aphis where no such phænomena are manifested*.

Léon Dufour, whose extent of research and comparison of the generative organs of insects led him to a true appreciation of the nature and function of the appendages to the female organs of the oviparous Aphides, referred the phænomena of the generation of the larviparous Aphides to 'spontaneous or equivocal generation.' Now if we consider what we actually learn from these words,—that the larvæ produced by the virgin Aphides are produced by 'spontaneous' or equivocal generation,—it will seem to be little more than another mode of stating the fact. The condition or mode of the fact, *i.e.* the phænomena rendering it possible, are not explained by them: M. Léon Dufour, however, meant to record his belief in a hypothetical mode of generation, in which, as he expresses it, 'the act of impregnation was in no degree concerned.' Having detected the male Aphis and well scrutinized the structure of its organs, having witnessed the coitus with the winged female, and carefully excluded the male in repeating the observations and experiments of Bonnet, M. Dufour satisfied himself, and affirmed, that impregnation had no share whatever in the phænomena of the development of the larval aphis in the body of another virgin larval aphis.

With regard to the hypothesis of spontaneous generation, the reasons which have led me to concur with most physiologists of the present day in rejecting it were fully given in

* Siebold, in Froriep's Notizen, Bd. xii. p. 308.

a former Course of Lectures on the subject of Generation, nine years ago, and every exact observation and experiment subsequently recorded serve to render that hypothesis less tenable and more gratuitous.

The learned and ingenious authors of the deservedly popular 'Introduction to Entomology' admit it to be "an incontestable fact that female Aphides have the faculty of giving birth to young ones without having had any intercourse with the other sex," and they suppose "that one conjunction of the sexes suffices for the impregnation of all the females that in a succession of generations spring from that union." They adduce, in order to show that such a supposition is not contradictory to the general course of nature in the production of animals, the case of the hive-bee, "in which a single intercourse with the male fertilizes all the eggs that are laid for the space of *two* years;" and the case of a common spider, showing "that the sperm preserves its vivifying powers unimpaired for a long period, indeed a longer period than is requisite for the impregnation of all the broods that a female Aphis can produce." But these instances do not touch the question how one of such a brood, insulated from all connection, should give birth to other broods. Admitting that this phænomenon may depend on the inheritance of the impregnating principle transmitted from generation to generation, the problem for the natural philosopher to explain is, how this is brought about. The superaddition of the 'spermatheca' to the vagina of the queen-bee, as of other oviparous insects, plainly accounts for the fact in the œconomy of that insect which Messrs. Kirby and Spence quote, according to the function of the part determined by the well-devised experiments of Hunter on the silk-moth*. To say that one conjunction of the sexes suffices to impregnate the females of the successive generations of Aphides springing from that union, is little more than a statement of the fact; and it

* On Bees, Philos. Trans. 1792, p. 175.

seems, indeed, to have been so felt by the able entomologists cited, who conclude their remarks by confessing,—"It is however one of the mysteries of the CREATOR that human intellect cannot fully penetrate*."

Prof. Morren, a comparatively recent observer of the anatomy and generative œconomy of the Aphides, and impressed by analogous feelings of the extreme difficulty of the problem, having accepted the hypothesis of spontaneous generation as it has been applied to the Entozoa, propounded, though not without reserve, a theory that the larval aphides were developed in the body of the virgin parent, like Entozoa, "by the individualization of a previously organized tissue †." Here also is a phrase which, when the meaning of it is analysed, does little more than express the old facts in a new way. When a larval aphis is developed, a new individual exists; in other words, it has been 'individualized'; and as nothing can come out of nothing, it must have been by the individualization of a previously existing something. The question to be solved is, what is that something, and what has happened to that something to make its individualization under the form of a larval aphis possible and conceivable by us according to the known analogies of other embryonic developments or individualizations? That would be the explanation of which we are in quest,—one going as far as the explanation which we are able to give, for example, of the development of an ordinarily impregnated ovum; and, by the proved analogy of the essential condition of the development in the virgin Aphis with that condition in the impregnated ovum, capable

* Introduction to Entomology, vol. iv. p. 161.

† "À dire vrai, je me refuse à émettre une opinion au milieu d'une tel dédale, et je tiens pour plus philosophique d'avouer son ignorance dans un phénomène où la Nature nous refuse même l'apparence d'une explication. S'il fallait une explication à toute force j'admettrais que la génération se fait ici, comme chez quelques Entozoaires, par individualisation d'un tissu précédemment organisé."—*Annales des Sciences Naturelles*, t. v. 1836, p. 90.

of having every advance of knowledge of the operation of such essential condition applied to it.

When however M. Morren affirms "que la génération se fait ici, comme chez quelques Entozoaires, par l'individualisation d'un tissu précédemment organisé," the objection immediately arises, that no one has ever seen a portion of mucous membrane, muscular fibre, or other organized tissue detach and transform itself into an entozoon: such a process is as gratuitously assumed, and as little in accordance with observed phænomena, as 'spontaneous generation' in the abstract. In a former Course I objected that "The fissiparous nucleated cells of the ovum, once metamorphosed into a tissue, can produce nothing higher, and nothing else save by their decay, which products are excreted: but the cells which retain their primitive state amidst the various tissues which the coalescing cells have constituted in building up the body of the new animal may, by virtue of their assimilative and fissiparous forces, lay the foundation for a new organism." I shall not however here pursue the argument which is carried out in my published 'Lectures on the Invertebrate Animals,' but shall proceed in the next Lecture to compare the phænomena of generation from virgin larvæ, and the successive production of many individuals from a solitary ovum, which other classes exhibit, and to consider the explanations that have been offered of such phænomena, and how they have been generalized.

LECTURE II.

On Parthenogenesis (*continued*).

In the former part of this Introductory Discourse I adduced some of the instances in the animal kingdom in which a species is propagated in different ways, and is represented by procreative individuals of different forms; the group of such individuals representing nevertheless one and the same species, and returning into itself. I cited the hypotheses which naturalists and physiologists of deservedly high repute had propounded for one of the earlier known instances of this cyclical generation, and showed how they failed in their end; and I proceed now to consider the explanations that have been offered by those who have recognized and pondered over a wider range of these phænomena, and have endeavoured to generalize them.

With a view to illustrate one of these generalizations, permit me to revert to some of the more simple manifestations of the phænomena which we were last considering.

Suppose the Monad to be developed from a germ-cell, and to propagate by spontaneous fission, each individual so formed developing and liberating germ-cells, and these again producing fissiparous individuals*; just as the Hy-

* On the authority of Ehrenberg. No one however has yet witnessed the development of the germ-cell into the Polygastrian; but this negative fact seems to me to have undue weight given to it when it is made to preponderate against the analogies which have led the masterly Micrographer to his conclusions. The germ-cells, which in well-fed Polygastria occupy the interspaces of the digestive sacs, the rythmical pulsatile sacs and the nucleus, are too regular in their cell-form, and for the most part too much alike, to allow of our dismissing them as of no functional significance under the name of 'sarcode.' M. Dujardin would seem also not to have comprehended the essentials of an ovum and of development from such, in the lowest forms of animals, when he objects to Ehrenberg's interpretation of the cells in question, "pour être fixé définitivement sur leur nature il faudrait avoir vu au moins des coques vides après l'éclosion." (Annales des Sciences Naturelles, t. x.

dra is developed from an impregnated ovum, and propagates by gemmation an individual which in its turn develops fertile ova. Not that the processes always do alternate with this regularity, but they may do so.

It is obvious that by calling them 'alternate generation,' we should not explain their nature any more than if we were to say that the polype from the bud, or the monad from the fission, was "spontaneously or equivocally generated independently of any impregnation," or that they resulted "from the individualization of a previously organized tissue." All these would be but so many different modes of expressing the fact, with the addition of demonstrable misconception of its nature by the advocates of the equivocal generation hypothesis.

Let us further suppose the hydra from the bud to assume a different form from the egg-born hydra out of which it proceeded, and to be oviparous; but the ova to produce only the lower form of hydra, which is gemmiparous; a lower and higher form alternately appearing, the one from an egg, the other from a bud. These phænomena might likewise be defined to be 'an alternating generation'; but

1838, p. 298; reproduced by Siebold, Lehrbuch der Vergl. Ana . p. 23.) Such an objection would have force only were a shell or chorion the essential part of an ovum. But this essentiality being the impregnated germ-cell, which alone represents the ovum in the Polygastria, it may be developed into the embryo, without the phænomenon of exclusion, as in the case of the monadiform embryo of the Medusa, and as Steenstrup describes to be the development of the gregariniform larvæ of the *Distoma tarda*. This is the course of development which might be anticipated in the representative of an ovum in a microscopic monad which itself represents an animated cell or ovum. The relation however of those minutest forms of Polygastria, *e. g. Chlamydomonas pulvisculus*, to the larger and more complex forms has still to be determined. If they should prove to be embryonic forms, the significance of their close repetition of the first stages in the formation of a germ-mass in the ova of higher animals by undergoing their spontaneous fission within a common covering would be intelligible. Compare fig. 14, p. 24, and figs. 33–44, p. 77, of my "Lectures on the Invertebrate Animals," 8vo, Longmans, 1843.

we should not, by that definition, have penetrated one step into the mystery of the development by the gemmiparous hydra of an offspring, without the preliminary act of impregnation in its own person.

Again: the simple hydra, which by gemmation produces the hypothetical higher form of oviparous hydra, may be designated a 'larva,' as containing potentially, and concealing, as it were by a mask, such higher form of animal. Or, by another figure of speech, the simple gemmiparous hydra may be called a 'wet-nurse,' in the character of carrying or contributing sustenance to a young individual of a higher grade than itself. But neither of these metaphors would convey to us an idea of the organic conditions essential to the development by the larval or nursing hydra of a bud producing another individual: they would prove, I opine, to every thinking mind, very unsatisfactory substitutes for such knowledge.

The terms *Generationswechsel*, 'alternate generation,' and *Amme*, 'wet-nurse,' have been, however, proposed by Dr. J. J. Sm. Steenstrup, a learned and ingenious Danish Professor of botany, in explanation of the "natural phænomena of an animal producing an offspring, which at no time resembles its parent, but which itself brings forth a progeny that returns in its form and nature to the parent;" and these phænomena, he writes, were "till now inexplicable" (p. 1), meaning until the publication of his work "Ueber den Generationswechsel," which has been translated by the 'Ray Society' with the title "On the Alternation of Generations, or the Propagation and Development of Animals through Alternate Generations, a peculiar form of fostering the young in the lower classes of animals," 8vo, 1845*.

I have carefully studied this work in the hope of obtaining some further insight into the mystery of Parthenogenesis, or procreation by an animal without sexual

* This is the edition cited in the present discourse.

concourse, beyond that which my observations on the Aphides in 1841 and 1842 had furnished me with*. But, although I laid down the volume with most grateful feelings towards the ingenious author for his useful collection of scattered memoirs detailing the phænomena, for his confirmation by personal researches of some of them, and his generalization of the whole, I sought in vain for any observation which really explained them, or anything purporting to be explanatory of them, save the phraseology and figurative expressions above cited: no organic condition is pointed out as being related or essential to the 'Lucina sine concubitu.'

With regard also to figurative language in science, unless the metaphor be exact, it misleads rather than explains.

Thus, as to the term *Amme*. The development of the secondary germ-cell in the body of a larva is at the expense of the surrounding cells and fluids of that larva, which therefore contributes food to the embryo; but this is rather as the mother of the viviparous vertebrate animal contributes nutriment to its embryo, than as the wet-nurse does to her foster-child: the relation of the offspring of the parturient larva to its procreator is also very different from that of the infant to the nurse that suckles and dandles it; and more closely resembles that of the fœtus *in utero*.

To rightly and clearly understand the phænomena we must adhere closely to them and to nature, and be careful not to be led astray by ambiguous or remotely figurative expressions.

No naturalist or physiologist has hesitated to call the polype which propagates by gemmation a 'parent' in relation to the young polype so propagated: it is true that the parent has produced without preliminary sexual intercourse in her own person, and she may have received *ab ovo*, and not herself have developed the germ-cell which was the essential basis of the bud; yet the term 'parent' is never-

* 'Lectures on the Invertebrate Animals,' pp. 233–235.

theless more appropriate than that of 'nurse.' And were the bud to be developed into a higher form of animal than that which produced it, the term 'parent' would still, as it seems to me, be the most appropriate one to designate the relation; since the bud, in regard to the individual producing it, would still be 'its own flesh and blood,' as the parental relation is expressed in homely parlance.

It is by no means easy, however, to find a name for the relation in which the fissiparous monad stands to the two monads between which it has been equally divided. A parent retains its individuality distinct from its progeny; but the monad has become a part, and indeed the chief part, of the two that have resulted from its spontaneous fission. Both separated moieties are, in an equal degree, the same individual as the whole from which they proceeded; and in an infinitesimal though conceivable degree the actual monad is the same individual as the first created one from which it may have proceeded by an uninterrupted succession of spontaneous fissions: and in that degree it may be viewed as one of the oldest individuals in creation, the individual having never wholly or bodily become deceased.

These phænomena, as you will perceive, are suggestive of reflections on personal identity and individuality which might exercise and perplex as keen wits as those of ancient Greece that debated the question of the identity of the old ship of Theseus which had undergone so much repair that no part of the original wood remained.

But the true and rational explanation of natural phænomena is usually the result of the exercise of common sense and careful observation; and, returning to those before us, I may recall to your recollection that the Medusæ actually manifest the phænomena that I have ascribed to the Hydra for the sake of illustration: that is to say, they resemble the polype at one stage of their development or under one form of individualization, and the medusiform

individuals are developed from segments separated from the larval polype. Analogous phænomena, as we have seen, are presented by some of the compound Hydriform polypes, by Echinoderms, by certain Entozoa, by compound Ascidians and Salpæ amongst the Mollusks, and, with various modifications, in other Invertebrata up to species of Insecta, where, in the Aphis, the 'Lucina sine concubitu' has ever excited the wonder if not the incredulity of those who for the first time have been made acquainted with the facts*.

The value of the 'alternate-generation' theory is well tested by its alleged power of affording the explanation of this very remarkable mode of Parthenogenesis. The virgin-procreation of the Aphides is described by Professor Steenstrup in his work (p. 108), agreeably with the account which I have already given and which is generally received. He calls the virgin larviparous Aphides, *Ammen*, or 'wet-nurses†'; says the species is propagated by 'alternate gene-

* "The multiplication of these little creatures is infinite and almost incredible. Providence has endued them with privileges promoting fecundity, which no other insects possess: at one time of the year they are viviparous, at another oviparous; and what is most remarkable and without parallel, the sexual intercourse of one original pair serves for all the generations which proceed from the female for a whole succeeding year. Reaumur has proved that in five generations one Aphis may be the progenitor of 5,904,900,000 descendants; and it is supposed that in one year there may be twenty generations."—*Kirby and Spence, Intr. to Entomology*, vol. i. p. 175.

† The adoption of the extreme metaphor of *Amme* was least to be expected from the physiologist who objected to the comparatively close and true application of the Linnæan figure *larva* to the answerable stage in the metamorphic parthenogenesis of the Radiata. "It is quite erroneous," says Steenstrup, "to term the *Scyphistoma* the larval condition of *Medusa aurita*, since a *Scyphistoma* never becomes a *Medusa*, but is the *quasi* mother of some scores of them." (p. 6.) Not more erroneous, however, than to term the wingless procreating Aphis a 'larva,' which may be the mother of a winged Aphis, without herself becoming one. Yet under certain conditions the 'larva' does become an 'imago,' as in *A. Coryli* and *A. Quercus*, e. g. It seems better therefore to extend, in like manner, the signification of the term 'larva' to

ration'; and affirms that "no true ovary has been discovered in the larval and larviparous Aphides, but that the germs, as soon as they are perceptible, are situated in organs which must be regarded as oviducts and uteri." (p. 112.) According to my own observations the germs are perceptible in the embryo Aphis, above the simple digestive sac, before any organs have been formed for their reception. And, with regard to the nature of the organs when formed, I may remark that the continuity of the ovarian tubes with the oviducts in all insects is such as to render the negation of the term 'ovary' to those two bodies from which the slender extremities of the eight oviducal and uterine tubes proceed in the larval Aphis, to say the least, quite arbitrary. My examinations agree with those of Siebold, in determining scarcely any appreciable difference between the ovaria of the oviparous and those of the viviparous females. The contents of the ovarian tubes differ, inasmuch as they contain oval masses of granules or nuclei, comparable to the germ-mass in its state of minutest subdivision, in the virgin aphides, and not ova with the germinal vesicle as in the oviparous females. The most marked and essential distinction, however, between the generative organs of these two kinds of female is the multilocular form of the uterus and simple vagina in the viviparous one, and the super-

those individuals in other classes that contain 'potentially' the higher form, and generate it by gemmation, than to restrict it to those that are actually themselves metamorphosed into such form, which metamorphosis is, after all, but a minor degree of metagenesis. Throughout Prof. Steenstrup's essay we meet indeed with instances where Nature, as it were, compels him so to use the Linnæan term or an equivalent; as *e. g.* where speaking of the larval Medusæ he writes: "But there is also a most essential difference between the *young fry* and the full-grown animal." "Let us now trace these *young Medusæ* further" (p. 14), meaning the individual or 'larva' in the mask of the 'planula' of Sir J. G. Dalyell. "This polypiform animal, which we shall afterwards consider as a *pedunculated Medusa*." (p. 15.) In what respect is it less erroneous, on Prof. Steenstrup's own argument, to call this *Scyphistoma* 'a pedunculated Medusa' than a 'larval Medusa'?

addition to the vagina of the oviparous copulating female of a sperm-sac and mucus-glands. In denying the presence of ovaria in the larviparous Aphis it would seem that Prof. Steenstrup had been biased by a predilection for the metaphorical name of *Amme*, which he applies to them, and by an *à-priori* conclusion, which he thus enunciates, viz. "that as in the more perfect females an *ovary* especially is formed, so in the '*nursing*' individuals a much-developed *uterus* is presented, in consequence of which, they, as individualized *uteri*, have assigned to them, as the object of their existence, the performance of the functions of a *uterus*." (p. 113.) And, no doubt, the relations of the larval Aphis to the embryo developing within it are much more truly uterine than mammary—more maternal than nutricial.

Some of the progeny of the primary germ-cell in the human species are discernible in the ovaria of the human embryo, and may have laid the basis of such ovaria, since the like unchanged progeny of the impregnated germ-cells have undoubtedly constituted the ovaria in the larviparous Aphis: only in the human embryo the spermatic virtue has been so far exhausted in the scanty remnant of the remote progeny of the primary cell, which remnant goes to form the ovarian germinal vesicles, that the stimulus of a new coitus is requisite to set on foot the developmental processes. In the Aphis, on the contrary, the presence of such common external stimuli as warmth, light and nutriment suffice to call in action the latent remnant of the spermatic virtue, and to produce such a multiplication of the derivative germ-cells and nuclei, as serves not only for the formation of the tissues of the embryo, but to spare; and such unmetamorphosed germ-masses are stored up in its ovaria with their inherited spermatic power, which, notwithstanding its reiterated subdivision, is still capable of responding to the action of the same external stimuli to which, as the exciting cause of the procreative act, the entire animal owed its origin. Had

the Danish physiologist rightly recognized the anatomical structure and contents of the generative organs of the larval Aphis, he might have discerned a much closer relationship between the ovaria and the act of larval propagation than between this and the uterus.

When, in regard to the analogous generation of the *Medusa*, Prof. Steenstrup says that the polypiform *Scyphistoma* "is a *precedent* generation of the kind in question," viz. 'alternate generation,' and that the *Strobila* "is a *precedent* individual or *preparative* individual," it seems to me that we have here only a different and more formal mode of expressing Siebold's and Sars's facts: viz. that the individual form of the *Medusa*, which Sir J. G. Dalyell called the *Hydra Tuba*, precedes the more perfect form, and that the next larval individual, which Sars called '*Strobila*,' is preparatory to the production of the young *Medusæ*.

It does not explain why the *Hydra* precedes the *Strobila*, or how the *Strobila* prepares the *Medusa*. The conditions of the organization that render the gemmation of the *Hydra Tuba* and the spontaneous multifission of the *Strobila* possible are not pointed out; these phænomena are left as unexplained as they were before: at least the words that "they take place agreeably with the law of alternate generation," and the metaphorical comparison of the *Hydra* and *Strobila* with 'wet-nurses' (*Ammen*), bring no information as to the organic conditions of the phænomena: the facts, as discovered by Sars and Siebold, remain just as absolute and empirical as they were before*.

They have, however, been grouped together with corresponding phænomena in other species, and some of their analogies have been pointed out for the first time by Prof.

* This the clear-headed Norwegian observer strongly felt when he asked:—"Und wie will man denn die Stolonenbildung, die doch deutlich genug und schon von Siebold an den achtarmigen Medusen-ammen beobachtet worden ist erklären?"—and was compelled to answer: "Davon schweight Steenstrup."—*Sars, Fauna Littoralis Norvegica*, fol. 1849, p. 14.

Steenstrup. These characteristics of his Essay have procured for it a wide and favourable reception; and the terms in which he has summed up the facts are now commonly received both here * and on the Continent in the sense in which he has proposed them, viz. as explanatory of the phænomena so generalized. It is against this arrest of inquiry and judgment that I now chiefly argue, from a conviction that a better explanation of the phænomena may be given, or, I should rather say, a real explanation, so far as it goes, as compared with the seeming explanation according to the terms of the 'alternate-generation' theory.

I am not, however, the only English physiologist who has submitted the true value of this theory to examination. The able author of the article on Sir John Graham Dalyell's beautiful work "On the Rare and Remarkable Animals of Scotland" in the 'Annals and Magazine of Natural History' (1848, p. 312), has pointed out some of the facts which he deems irreconcileable with Steenstrup's theory: and Dr. Carpenter, in a valuable paper on the same subject in the Medico-chirurgical Review, 1848, has rejected the theory in stronger terms of condemnation than I think are applicable to it. The latter reviewer says that Steenstrup "has built up a very plausible hypothesis upon the foundation of the phænomena of metamorphosis presented by the zoophytes and acalephæ," and characterizes it as "a very premature, erroneous and limited expression of the real facts" (p. 192); affirming that "Professor Steenstrup has laboured under a total misconception of the most important part of the process" (*ib.*), his propositions being "totally inapplicable to the vegetable kingdom." And Dr. Carpenter offers what he believes to be "a

* "I see no reason, therefore, to dissent from the theory of Steenstrup: it is the simplest and most intelligible, as well as the most original expression hitherto offered of the astonishing facts which he was the first to generalise." Prof. Ed. Forbes, 'Monograph on the Naked-eyed Medusæ,' p. 88.

clearer and more philosophic view of the subject" (p. 193). This view may be briefly stated to be based upon the belief that 'gemmiparity' or the process of gemmation is 'altogether distinct' from oviparity or the process of development in and from an ovum; viviparity being rightly shown by the reviewer to be a mere modification of the process of development from an ovum (pp. 193 and 194).

Oviparity "is effected by the concurrent agency of two sets of sexual organs, situated on the same individual or appertaining to two different beings;" and "where there is no evidence of such concurrence, the presumption is" held to be "strong that the reproduction is really carried on upon the gemmiparous plan," which is defined as "a multiplication of cells by a process of *continuous growth*." (p. 193.)

Before entering into the inquiry how far what is known of the process of gemmation is rightly defined as one of 'continuous growth,' as contra-distinguished from the growth of the germ-mass and embryo in an ovum, I feel desirous to offer a few remarks in mitigation of the censure which Dr. Carpenter has passed on the ingenious Essay on the Alternation of Generations.

When Prof. Steenstrup, for example, in reference to the classes of Invertebrate animals whose generation he has described from his own or others' observations, says that the offspring never resembles its immediate parent, and that the parent "does not meet with its resemblance in its own brood, but in its descendants of the second, third, or fourth degree," he simply enunciates a matter of fact, and sets forth no hypothesis plausible or otherwise. Unless it can be shown that the ovum of a Medusa does not produce a Hydra Tuba, and this a Strobila from which the Medusa ultimately comes; and unless the cercariform individual which intervenes between the gregariniform one and the Distoma, developing the ova of the Entozoa of the freshwater Snail, have no existence in nature, the language of the 'alternate-generation'

theory cannot be justly described as "a very premature and erroneous expression of the real facts." It merely disappoints the expectation raised by Prof. Steenstrup as to its affording an explanation of the facts. And inasmuch as the seed of a plant produces a leaf and its root, which proceeds to develope other leaves before it finally produces the flower with the seed like that from which the first cotyledonal leaf or pair of leaves originated; and since therefore the plant-individual, in the form of a leaf, intervenes between the seed and the male and female individuals, called 'stamens and pistils,' concerned in the reproduction of the seed, the generation of such plant, as Prof. Ed. Forbes has well argued*, may be called 'alternate,' in the sense in which Steenstrup applies the term to the generation of the Medusa and the Aphis; and such language, it seems to me, would be very far from implying "a total misconception of the most important part of the process," though it might not necessarily involve a full and clear recognition of its nature or essential condition.

The reviewer defines this part of the process to be 'growth in continuity with the parent,' effecting gemmation and also spontaneous fission, in contradistinction to 'multiplication by means of germs detached from the parent.' But the nuclear germ-mass in the virgin larviparous Aphis is as really distinct and detached from the parent as the germinal vesicle which is developed into an egg in the wedded oviparous Aphis. In this, when impregnated, a germ-mass must be formed, identical in character with the foregoing, prior to embryonic formation. The first steps of development are identical in both: they might equally be defined as "a multiplication of cells by continuous growth and independent vitality;" but this definition would be simply an expression of the well-known fact that cells do multiply, and especially germ-cells, and so produce what may be called 'continuous growth,' as in

* *Loc. cit.* p. 87.

the Confervæ, and that both the cells and the parts they form have vitality. What we are in quest of is the condition of such growth by multiplication of cells, which is essential to their forming a germ-mass and laying the foundation of a future individual; and our conception of this condition will be in the ratio of our comprehension of the purport of the process by which the germ-mass is formed in all animals.

When we find the development of the Aphis by multiplication of cells, and its continuous growth by the metamorphosis of the resulting germ-mass, taking place within the body of the larval Aphis, without the concurrent agency of male and female sexual organs, and without any previous detachment of an ovum properly so called, or any pre-existent ovum, like that in the larviparous Blue-bottle Fly, we recognise a phænomenon essentially similar to the process which by multiplication of cells in so-called 'continuous growth' developes the uncinated and suctorious head and neck from the common cyst of the *Cœnurus**, and which produces the bud in the adult *Hydra viridis* and in the larval *Hydra Tuba*. But in the Aphis the gemmation, instead of protruding through the side of the abdomen, extends into an oviduct; the progressive growth distends the tube into a uterine sac, and the progeny escapes 'per vaginam.'

The presence of female organs determines the sex of this viviparous larva, and by this analogy Prof. Steenstrup may have been guided to the opinion that the gemmiparous larvæ of the Medusæ and other species, which he calls 'Amme,' were females. Dr. Carpenter affirms that "he had no more reason for so calling them than the botanist would have in speaking of a budding plant as of the female sex up to the time of the evolution of the flowering system." (p. 194.) And this will seem to be true to the botanist who may view such a plant as an individual whole, with its nutritive,

* H. D. Goodsir, 'On the Development, &c. of the Acephalocysts,' Trans. Royal Soc. of Edinburgh, 1844, vol. xv. p. 565, pl. 16.

respiratory and generative organs, comparable to those in a complex animal. But the true test of any opinion as to the sex of a gemmiparous larva can only be applied and appreciated by the physiologist who has learnt to view the relations of the plant to the animal in the spirit of John Hunter*. If the budding polype be analogous to the leaf and leaf-bud on the one hand and to the larviparous Aphis on the other,—if these be severally examples of true gemmiparous individuals differing only in the scale of their complexity,—then the analogy of the Aphis would justify the opinion that the budding polype is essentially female. And if it can be proved that the growth by cell-multiplication producing a bud, instead of being 'altogether distinct from' the growth by cell-multiplication in an egg, is essentially the same kind of growth or developmental process, that same analogy will furnish the botanist with a reason that he perhaps had not before, for viewing a budding plant as essentially 'female,' and for regarding the so-called males of the Palms and other Linnæan *Diœcia*,—plants which terminate their series of successive gemmations by elaborating the true male individuals or 'stamens,'—as stem-bound aggregates of female gemmiparous individuals in the form of leaves and buds; and these, by the light of zoological analogy, may be viewed as 'larvæ' in comparison with the more advanced and more individualized stamens or males associated with them.

The green petiolate discoid 'gemmæ' of the Liverwort (*Marchantia polymorpha*), which are detached whilst in the condition of a mere aggregate of cells in an envelope, the

* "In the vegetable this power or mode of propagation arises from two principles; one is that every part of a vegetable is a whole; the second arises from some having the power in every part (under certain circumstances) of retaining life, bringing in nourishment at every part, and of producing parts called roots. So that a vegetable under these circumstances is capable always of being multiplied as far as it can be divided into distinct plants."—'Introduction to the Organs of Generation,' Physiological Catalogue of the Hunterian Collection, vol. iv. p. 4.

'spores' that are thrown off from the tissue of the fronds of ferns, and the 'bulbels' that drop from the axils of the *Lilium bulbiferum*, are precisely analogous to that aggregate of cells in an envelope that falls into the anterior chamber of the locular uterus of the virgin Aphis: only in the plant the aggregate of cells is detached from an external surface, but in the animal from an internal surface.

When it is asserted that in the propagation of the Hydra by buds or by artificial division there is not 'anything like oviparous reproduction,' but that it is the result of the simple action of *continuous growth*, we feel the want of a clear definition of the meaning of that phrase. In the growth of the Conferva, which the reviewer rightly admits to be analogous to that of gemmation, each filament originates from a germ, which is first developed into a single cell; this cell increases, and it either divides, or its germ-granules give origin to two cells within it, which take the place of the former; and by the repetition of this increase and multiplication a long and single series of tubular cells, attached at one end, free and constantly growing at the other, is at last produced, as Unger and other mycologists have clearly demonstrated.

Now, short of the mere formal and non-essential modification of the juxtaposition of the cells, end on end, the process here described is the same as that with which the development *in ovo* of the mammal, and doubtless also of Man himself, begins: the germ-cell gives origin to two; these new cells themselves undergo the same increase by subdivision, which is repeated through a long series of cell-generations until a coherent mass or body of countless cells is produced, which differ from those in the Conferva, inasmuch as they are in contact with each other at many and indefinite points, instead of being arranged in a linear series.

The first step in the formation of the bud in the Hydra, as in the Cœnurus, is the multiplication of cells, which also are aggregated together as in the ovum, and not set end on

end as in the Conferva. The mutual contact of these delicate cells suffices for mutual action and reaction on one another; excess of nutriment or other quality in one is balanced by the endosmotic action of neighbouring cells, just as the nutriment is transmitted from cell to cell to the last developing-cell in the chain forming the conferval filament.

The young Hydra from the bud is identical in organic structure and character with that which comes from the ovum: and when the effects of organic development are the same, their efficient causes cannot be 'altogether distinct': only the non-essential accessories of the process may be the subject of variation.

The retention of unused-up germ-cells in the tissues of the Hydra is the condition which explains the fact, that, when favourable external circumstances of light, heat, and food concur, it may be propagated by buds. It is not, however, absolutely correct to say that buds "may arise from any portion of the body of the parent structure;" in the *Hydra fusca*, at least, they are pretty constantly developed from a special part of the animal, as was long ago shown by Roesel*, and has been recognized by all subsequent observers: the part in question is at or near to the bottom of the digestive sac; between it and what might be termed the foot or attaching pedicle of the polype;—and this is precisely the part where those nucleated cells are assembled in greatest number, which most closely resemble the secondary or derivative germ-cells in the ovum.

It might be specified as the 'ovarium' of the polype, but that the true ova are matured from cells not situated exclusively at this part; nevertheless the germ-cells situated between the stomach and pedicle are the essential elements of ova, and are only not converted into ova, and cast off with a chorion, because their development proceeds directly and at once to the business of the formation of an embryo: and

* See his beautiful 86th plate in the 'Historiæ Polyporum,' of the Supplements to the 'Insekten-Belüstigüngen.'

the difference between this mode of generation and that of the virgin larviparous Aphis is merely in the protrusion of the embryo in the one case through the skin, and in the other through the vagina: both secondary modifications or non-essential accidents of the generative process. In suffering to pass uncorrected the term 'ovum,' applied figuratively to these germ-cells of the budding Hydra, in a former Course of Lectures*, published too hastily perhaps, as they were reported by Mr. Cooper, I freely confess that I was justly amenable to the criticism, based on the fact that a true ovum with a bristled chorion had not been shown to exist at the base of the bud. What I believe myself to have stated was, that the true ovum of the Hydra had received the influence of the spermatozoon, and that the primary germ-cell had divided that influence amongst its progeny, which stood in the same relation to the bud as the corresponding derivative germ-cells were afterwards explained to stand to the offspring of the virgin Aphis †.

No buds are developed from the complex tentacles of the Hydra. Those cells that have been metamorphosed into tissues have lost the power of reproducing anything but those tissues or the products of their decay. Had this truth been apprehended by Morren, he would not have imagined that an entozoon could result from the individualization of a previously organized fibre. Many derivative germ-cells and nuclei are retained in the body of the Hydra, each being, in its degree, impregnated; and this I continue to regard as the condition of its power of gemmation, and also of the fact, that when cut into numerous parts, many Hydræ may be thus artificially propagated.

The reproduction of parts of higher animals has also been found to depend on pre-existing cells retained as such. Mr. H. D. S. Goodsir has shown that in the Lobster *e. g.*, so noted for the power of reproducing its claws, the rege-

* 'Lectures on the Invertebrata,' 8vo, 1843, p. 85.

† Ibid, pp. 234, 366.

nerative faculty does not reside at any part of the claw indifferently, but in a special locality at the basal end of the first joint of each of the legs. This joint is almost filled by a mass of nucleated cells surrounded by a fibrous and vascular band; and other nucleated cells intervene between this band and the outer crust. The vessels of the band pass onwards for about half an inch and return upon themselves, forming loops. When a claw is broken or otherwise injured and disabled, the Lobster or Crab, by a violent muscular effort, casts it off at the transverse ciliated chink or groove which indents the reproductive segment. The new claw is developed by the multiplication of cells, which are soon divided into five groups answering to the five joints of the future limb: these nascent joints are folded upon each other in the Crab, but extended in the Lobster: in both they are at first enveloped in a sac formed by the distended cicatrix; the budding limb ultimately bursts this cicatrix and its growth is rapidly completed: a great proportion of the reproductive cells contained in the basal extremity of the injured limb, is used up in the production of the new limb; but a mass of them is retained unchanged at the basal joint, and ready to renew the reproductive process when needed. In the lower Crustaceans such groups of cells are found at more numerous joints.

Like Sars, the author of the article in the 'Medico-chirurgical Review' observes, with regard to Professor Steenstrup's account of the propagation of the medusiform from the strobiliform individuals:—"How these young ones are developed—whether from ova or from gemmæ—he does not attempt to explain; nor does he show, if they are produced from ova, by what male influence they are fertilized." (p. 204.) Steenstrup had not, in fact, any more than his reviewer, recognized the nature of the process consequent on fecundation, which carries the male influence through successive generations of larvæ. Yet he had persuaded himself that he was elucidating natural phænomena

which until his time had been 'inexplicable'; quite unconscious, apparently, how little the term 'alternation of generations,' and the figurative expression of 'wet-nurse,' applied to the fertile larval stage of an animal, serve to acquaint us with the nature or essential conditions of the phænomena. And I may further observe, that if it were proved that the 'multiplication of cells by a process of continuous growth, with independent vitality,' was a process altogether distinct from that multiplication of cells in an ovum which precedes the formation of the tissues of the embryo; yet the words 'multiplication of cells, with or without continuous growth,' would equally leave us devoid of the idea of the essential force and condition of structure that make the development of a young animal from a larval polype or a wingless virgin Aphis possible. And we are interested to learn, therefore, what that may be which the reviewer calls "our philosophical interpretation of this wonderful process" (p. 203). He truly compares the fertilized ovum of the medusa-parent to the *seed* of the plant, the polype that grows from it with its progeny by gemmation to *leaf-buds*, and those discoid portions developed between the base and summit of the Strobila to *flower-buds*. For these discoid segments, in point of fact, when separated, become either male or female Medusæ, and developing the generative organs, justify the above comparison. The reviewer says, "It is evident to us that the pile of medusa-discs is *not* formed by the constriction of the proper body of the original polypoid animal;" yet he afterwards states that the detachment of those discs "involves the separation of the tentacular ring from the body at the base,"—that it separates one end of the polypoid animal from the other,—which implies something more than constriction,—constriction, viz. carried to the extent of absolute fission of the original polypoid animal. But this fission is preceded, as in the Nais and Nereis, by gemmation of the part to be separated thereby.

There is doubtless a close and beautiful analogy between the stages of the development of the Medusæ and those of the Tree; between the larva of the one and the leaf of the other, between the ovum of the animal and the seed of the plant. Yet this comparison does not explain the essential condition of gemmation in either: one thing unexplained cannot be made to illustrate another unknown thing. One seems to get some knowledge when it is stated that the leaf is produced 'by continuous growth,' and that the bud of the Hydra is produced like the leaf. And had the reviewer recognized the essential concordance between the 'continuous growth' of the conferval filament and that which augments the germinal mass in the ovum, he might have arrived at the desired explanation; but he affirms them to be 'altogether distinct.'

Admitting the obvious analogies between the reproductive phænomena of the Medusa and the Plant, Dr. Carpenter says, "the whole of these phænomena appear to us to constitute but a *single* generation, instead of making *two*, as represented by Steenstrup;" and, availing himself of the popular idea that a tree is one individual living thing, he turns those analogies with apparently great power against the definitions of Professor Steenstrup.

It is quite true, as the able reviewer says, "that men are not in the habit of speaking of leaf-buds and the flower-buds of a plant as of two distinct generations." But before the whole doctrine of the 'alternation of generations' is knocked to the ground (p. 205), those who desire to secure for the ingenious Danish Professor the credit which he really merits, may bring to his support that other and perhaps truer interpretation of the phænomena and analogies arrayed against him, to which I have before referred in regard to his opinion of the sex of the budding polype.

The fertilized ovum of the medusa-parent is like the fertilized ovum of the Aphis, and the polype that grows from it resembles the first larva into which the embryo Aphis

expands. From this larva are produced other wingless larvæ, which are repetitions of the producer or parent; these larvæ in the Aphis remain disconnected from each other, and do not combine to form a compound structure as in certain zoophytes; they become detached like the bulbels of the *Marchantia* or the lily, only they are rather more advanced in individual development. But under certain conditions a new and different series of embryos forming male and female perfect insects are produced: these too become detached, and by their inherent power of movement, through the possession of wings, they carry the germs of a new generation to a distance from the plants which their larval parents have devastated. The whole of these phænomena appear to me, as they did to Bonnet, Reaumur, Dufour, and Morren, to constitute a succession of generations,—seven, nine, or it may be eleven. But as all the larvæ are like each other, they collectively represent with the perfect insects two generations, in respect of form, and the generation of larviparous and the generation of oviparous Aphides may thus be said to alternate with each other, in accordance with Steenstrup's general expression of the fact.

Now no physiologist has ever defined the series of virgin larviparous Aphides, with the ultimately produced winged males and oviparous females, as constituting a single generation, or the generation of the parts of one and the same individual; nor, if my comparison be true, have we better grounds for so defining the succession of distinct animals which have received the names of *Hydra Tuba*, *Strobila*, and *Medusa*, or the succession of those which have been called ciliated gemmules and planulæ, digestive polypes, generative polypes, Tintinnabula or free medusiform polypes of the Campanularia and Coryne; or the successively developed cotyledons, leaves and flowers of a plant which are combined by the stem into a seeming individual whole.

The analogy between the procreating larvæ of the *Aphis*,

the *Medusa*, and the *Coralline* is so true and so close, that if the larval Aphis be a distinct individual and not a part, so must be the strobila, the planula, and the gemmiparous leaf: if the succession of larval Aphides produced without the access of the male be truly described, as it always has been described, as a succession of generations, so must that succession of planula, polype and strobila which leads to the oviparous Medusa: and that succession of planulæ and nutritive polypes which precede the detachment of the free procreative medusoid polypes in the Coryne, and the like with the plant-generations preceding the flower.

The Botanist, in fact, arrived earlier than the Zoophytologist at an intimate philosophical comprehension of the nature of his composite subjects. After Linnæus had made known with his characteristic terseness and brevity the phænomena of the transformation of the leaf into the bract, the sepal or the petal, and the retrograde change of the stamen into the petal, of the petal into the sepal, and of this again into the leaf, in his '*Philosophia Botanica**,' and with more detail in the '*Prolepsis plantarum*†'; and when the great Goethe had gathered together these and other analogous phænomena in vegetable life, and had combined them harmoniously, with true poetic insight into their essential nature, in his famous doctrine of 'Vegetable Morphology,' a reconsideration of the nature of the essentially individual plant could hardly fail to suggest itself to the thinking mind.

* "Principium *florum* et *foliorum* idem est.
Perianthum sit ex connatis foliorum rudimentis.
Derivato nutrimento ad squamas amenti, destructis flosculis, mutantur in *Folia*.
Derivato nutrimento ad flosculos amenti, fiunt folia *Calyces*.
Luxurians vegetatio folia e floribus continuando producit.
Macra vegetatio flores e foliis terminando producit."—*Metamorphosis Vegetabilis*, Philos. Botan. p. 301.

† "Quando flos nascitur abeunt folia gemmacea anni sequentis in bracteas, tertii in calycem, quarti in petala, quinti in stamina, sexti in pistilla, quod a situ judicatur."—*Amœnitates Academicæ*, vol. vi. (1789) p. 341. The hypothesis of the succession has long been abandoned.

The 'Ur-pflanze' or ideal type-vegetable with which the 'Morphologie' of Goethe is illustrated (pl. iii. of the French translation) is an aggregate of modifications of the primitive type, not the fundamental pattern-plant itself. My idea of such, from the analogy of the typical vertebra or vertebrate skeleton*, is attempted to be expressed by the more simple forms associated together in the Frontispiece, fig. 1, and the nature of the association of the more or less modified individual plants is illustrated by the accompanying figures from the animal kingdom. The archetypal form of plant (phyton) nowhere perhaps exists in actual nature, but is presented under various modifications adapted to different conditions and functions, and deviating from the archetype as those functions become exalted. The most familiar, if not the commonest form of the individual plant, is the leaf, and it is sometimes cited as the archetypal form. In the specimens of Bryophyllum from the Physiological Series of the Museum (Nos. 2225 A & B), you may perceive the manifestation of the power of reproducing other individuals by the buds which have been developed from the angles of the marginal crenations of the leaf: in No. 2225 C. the buds have developed individuals having the same form as the parent, viz. the leaf, and they have sent down an organ for independent nutriment called 'root.' I long ago pointed out in our Physiological Catalogue (vol. iv. p. 8), with regard to those very specimens, how characteristic of the leaf-individuals which enjoy unusual power of gemmiparous reproduction it was to retain much of the primitive cellular structure.

The leaf, however, chiefly energises in the respiratory function, with which also a nutrient power is combined, since carbon is absorbed: with the leaf is connected that slender chain of sap-vessels and air-tubes which is continued from its petiole down to the root, and forms part of the same individual with the leaf: and the aggregate of

* On the Archetype and Homologies of the Vertebrate Skeleton, pl. 2, 8vo, Van Voorst, 1847.

these vessels, with a common condensed integument or 'bark,' constitutes the branches and trunk of the compound whole, which is called 'Tree.' A generation of leaves, the breathing parts of the individual phytons, perishes each year; but not before each individual has made preparation for its successor by developing a bud at the axil of the leaf, which remains when the leaf falls, and supplies its place in the following year. Here the individuals are successively propagated by gemmation, as in the Hydra and *Tubularia indivisa*, but continue associated together like the compound polypes. In order to effect a multiplication of plants at a distance from the parent, the common respiratory and gemmiparous form must be developed into a higher condition of individual plant. This begins by the suppression of the bud at the axil, and by the consequent concentration of the formative force in the act of metamorphosis and individual development. The 'whorl,' or group of such leaves in verticillate arrangement, constitutes what is termed the 'calyx': the calyx, then, consists of a group of metamorphosed and often more or less connate or confluent individuals, usually deprived of the power of gemmation: but their tendency to resume the more typical form of the individual—the leaf—must be familiar to all who have looked at this part in the proliferous roses. The cowslip shows the small amount of change which converts a leaf into a sepal.

The corolla consists of a whorl of more modified 'leaves,' called petals; and incloses a third 'whorl' of still more metamorphosed forms of the archetypal plant, called stamens: in these we see that development has advanced to the establishment of the true male individual, which, like the male in the Lernæa according to Nordmann, the male of the Argonaut according to Kölliker, and the male of the Rotifer according to Brightwell* and Dalrymple, is restricted almost to the function of elaborating the fertilizing

* 'Fauna Infusoria of Norfolk,' pl. 1. p. 2.

principle. Finally, we have the energies of the successive generations of the compound plant exhausted in the perfection of the female individual, the pistillum, with its ovarian base: the true nature of which is manifested by its common return to the more archetypal form of petal or leaf in those over-nourished plants that produce double flowers, *e. g.* the Ranunculuses, Saxifrages and Wall-flowers.

The ovule is perfected in the part called 'ovary,' forming the base of the female individual plant. By the passage of the pollen-tube to the foramen of the ovule, as traced by Brown in the Orchids and Asclepiads, impregnation results, and various beautiful contrivances exist for conveying the impregnated seed to a distance, where it may lay the foundation of a new series of united gemmiparous individuals.

I am quite sensible that the composite plant or the composite zoophyte, and the phænomena of their development, may be explained agreeably with ordinary ideas and common belief in regard to trees; viz. that the leaves are parts of a whole, that they are the respiratory organs of the tree, and the polypes the digestive organs of an individual compound organism. And this explanation agrees with the functions performed by the variously modified individuals in relation to the association; just as the several members of a regiment or a corporation constitute one organized whole. The question, however, is, whether the tree represents such a whole, or is equivalent to one of the organized individual members; whether the leaf and the stamen may not answer rather to different individuals of the 'body corporate,' than to the lung or the testis of any single individual. Unquestionably our choice of explanations ought to be governed by the results of the most extended and accurate analogies. Our first (and the common) notion of a tree and a coralline, as being respectively individual organisms, derives seeming support from the fact that in each species of composite plants and animals the aggregate of individuals assumes a de-

finite or specific form, whence the terms 'Oak,' 'Ash,' and 'Bell-coralline,' 'Fern-coralline,' 'Sea-oak-coralline,' &c. But, by parity of reasoning, the nests or 'combs' of certain Hymenoptera and the nidamental capsules of most testaceous mollusks might be regarded as individuals; for the separate ovigerous cells, of which they are respectively the aggregates, are grouped together in each species, in so constant and specific a form, as to be readily recognized after having been once defined.

It would have been strangely at variance with that beautiful principle of variety in non-essentials which pervades nature, if the individuals of different species of plants and animals, which cohere together after gemmation, had not been grouped each after its own specific pattern; but this specific pattern of grouping no more constitutes a single organic individual than it does in the case of the aggregate of egg-capsules or larval cells just cited.

If, however, it should still be felt that the explanation I have here offered in accordance with the opinions of Hunter*, Steenstrup†, Prof. Ed. Forbes‡, and other philosophic naturalists, be somewhat forced or at least optional, we may arrive perhaps at greater confidence in its exactitude by extending the bounds of the analogies by which it has been illustrated.

To facilitate the comparison I have devised the diagrams engraved in the frontispiece, Plate I.

* *Loc. cit.* "Every part of a vegetable is a whole." The enunciation of the idea is perhaps too general and extreme.

† *Loc. cit.* "It is certainly the great triumph of morphology that it is able to show how the plant or tree (that colony of individuals arranged in accordance with a simple vegetative principle or fundamental law) unfolds itself, through a frequently long succession of generations, into individuals becoming more and more perfect." (p. 114.)

‡ "We are not in the habit of regarding a leaf as the individual—popularly we look upon the whole plant as an individual. Yet every botanist knows that it is a combination of individuals, and if so, each series of buds must certainly be strictly regarded as generations."—Monograph on British Naked-eyed Medusæ, p. 87.

The pollen-tube or filament (*a*, fig. 1) discharged from the pollen-cell (*a'*) in the plant represents the spermatozoon (*a*, figs. 2 & 3) in the animal: its contents—whether by endosmose or perforation is immaterial—are received by the ovule (*b*, fig. 1), which is afterwards discharged and becomes free. Under favourable circumstances the formation of the embryo takes place, with manifold modifications, but essentially by the multiplication of cells, according to a process which is as much entitled to be called *continuous growth* as that process in the formation of the Conferva. The embryo (*c*) proceeds to develope the radicle and the plumula (*d*) by the metamorphosis and coalescence of certain of the impregnated cells, retaining the major part, however, as cells: and thus the first individual plant, or pair of individuals as in Dicotyledons, is established.

The ovum (*b*, fig. 2) of the zoophyte proceeds to develope its free locomotive embryo (*c*) by an analogous multiplication of cells, certain of which are metamorphosed into an external skin with vibratile cilia: the embryo settles, subsides, shoots out rays, analogous to the radicle of the plant, but for attachment only, and grows afterwards, as a stem, from which a polype (*d*) is speedily developed answering to the first cotyledonal leaf, or leaves, in the plant (*d*, fig. 1). Both plant and zoophyte proceed to develope by gemmation, the one a succession of leaves (*e e*), the other of polypes (*e e*), associated by the continuous growth of the connecting parts: and finally the plant by a metamorphosis of part of the stem and certain leaves produces the flower or fructification (*f*, *g*, *h*, *i*), and the zoophyte by a modification also of its stem and certain polypes produces an 'ovarian vesicle' (*f*) or a modified polype (*g*), or a medusiform individual (*l*), which is set free: in both cases the end to be attained is the diffusion of the species by means of impregnated seeds or ova.

Now, if we compare with the preceding the third figure (fig. 3), in which I have represented the corresponding

stages intervening between the ovum and the perfect male and female individuals of the Aphis, the analogy between these stages in the plant, the polype and the insect, will be seen to be both true and close. The spermatozoon (*a*) of the male Aphis (*h*) answers to the pollen-filament (*a*, fig. 1) of the male leaf or 'stamen' (*h*). The ovum (*b*) of the female Aphis (*i*) answers to the ovule (*b*) of the female leaf or pistil (*i*): by their combination the impregnated ovum results. The same processes of cell-formation ensue, and the embryo Aphis (*d*) is formed by the combination and metamorphoses of certain of these secondary germ-cells; but it retains the rest as a germ-mass in its interior, which may be compared with the cells of the pith of the plant, and with the cells or nuclear granules in the corresponding more fluid part of the pith of the polype. Under favourable circumstances of nutriment and warmth, certain portions of the retained germ-mass repeat the process of embryonic formation, and a larval individual (*e*, fig. 3) like that from the ovum is thus reproduced; which is only not retained in connexion with its parent, because the abdominal integument is not coextended with it.

The generation of a larval Aphis may be repeated from seven to eleven times without any more accession to the primary spermatic virtue of the retained germ-masses than in the case of the zoophyte or plant: one might call the generation an 'internal gemmation,' but this phrase would not explain the conditions essential to the process, unless we previously knew those conditions in regard to ordinary or external gemmation.

At length, however, the last apterous or larval Aphis, so developed, proceeds to be 'metamorphosed,' as it is termed, into a winged individual, in which only the fertilizing filaments are formed, as in the case of the stamens of the plant (*h*); another larval Aphis (*i*) perfects the female generative organs* and developes the ovules, as in the case

* This is not attended by the acquisition of wings; or, if they be de-

of the pistil (*i*). We have, in fact, at length 'male (*h*) and female (*i*) individuals,' preceded by reproductive individuals (*e*, *e*) of a lower or arrested grade of organization, analogous to the gemmiparous polypes of the zoophyte (*e*, *e*, fig. 2) and the leaves (*e*, *e*, fig. 1) of the plant.

I have described the process for its better intelligibility in the Aphides as one of a simple succession of single individuals, but it is much more marvellous in nature. The first-formed larva of early spring procreates not one but eight larvæ like itself in successive broods, and each of these larvæ repeats the process; and it may be again repeated in the same geometrical ratio until a number which figures only can indicate and language almost fails to express, is the result. The Aphides generated from virgin-parents, by this process of internal gemmation, are as countless as the leaves of a tree, to which they are so closely analogous.

It generally happens that the metamorphosis which I have described as occurring after the seventh or eleventh generation takes place much earlier in the case of some of the thousands of individuals so propagated (*k*, fig. 3): just as a leaf-bud near the root may develope a leaf-stem, a flower and seed-capsule (*k*, fig. 1) with much fewer antecedent generations of leaves from buds than have preceded the formation of the flower at the summit of the plant; or just as one of the lower and earlier formed digestive polypes may push out a bud to be transformed into an ovarian sac (*k*) and a generative medusa (*l*). The analogy is beautifully and closely maintained throughout.

The wingless larval Aphides are not very locomotive; they might have been attached to one another by continuity of integument, and each have been fixed to suck the juices

veloped in the oviparous female they soon fall. I have, however, retained them in the diagram for the better illustration of the analogy. Many of the virgin viviparous Aphides acquire wings, but never perfect the generative organs.

from the part of the plant where it was brought forth. The stem of the rose might have been incrusted with a chain of such connected larvæ as we see the stem of a fucus incrusted with a chain of connected polypes, and only the last developed winged males and oviparous females might have been set free. The connecting medium might even have permitted a common current of nutriment contributed to by each individual to circulate through the whole compound body. But how little of anything essential to the animal would be affected by cutting through this hypothetical connecting and vascular integument and setting each individual free! If we perform this operation on the compound zoophyte, the detached polype may live and continue its gemmiparous reproduction. This is more certainly and constantly the result in detaching one of the monadiform individuals which assists in composing the seeming individual whole called 'Volvox globator'; and so likewise with the leaf-bud. And this liberation Nature has actually performed for us in the case of the Aphis, and she thereby plainly teaches us the true value or signification in morphology of the connecting links that remain to attach together the different gemmiparous individuals of the volvox, the zoophyte, and the plant.

The popular notion of a plant, as we have said, is that it is one individual complex organism, of which the root answers to the nutrient system, the trunk and branches to the skeleton, the leaves to the lungs, and the flowers to the generative organs of an animal: but we never see the stomach converted into a lung, the lungs converted into a testis or ovarium, or reciprocally, as we trace the leaf changed into the stamen, or this by retrograde metamorphosis brought back to the state of a leaf. The stomach of a man if detached would not live and reproduce its kind like the polype of the Sertularia or the monad of the *Volvox*; nor would the lung manifest its individuality like the leaf of the Bryophyllum under similar circumstances. No!

A flowerless plant is an associated colony of simple organized individuals (phytons) propagating by gemmation.

A flowering plant, with stamens and pistils in the same flower, is not a hermaphrodite individual; but is an organically associated colony of phytons, most of which are simple and gemmiparous, but some through a higher energy have been developed into distinct male and female individuals.

The so-called male of the Diœcious plants is an organically associated colony of gemmiparous phytons with true male individuals; and the so-called female plant is a similar colony of gemmiparous phytons with true or perfect female individuals.

From plants to Aphides inclusive the phænomenon of Parthenogenesis is presented under manifold modifications, alike in this essential that they are all examples of organized beings from the impregnated ovum of which many individuals may be successively developed.

In the Vertebrated and in the higher Invertebrated animals only a single individual is propagated from each impregnated ovum. Organized beings might be divided into those in which the ovum is uniparous, and those in which it is multiparous. This is the first and widest or most general distinction which we have to consider in regard to generation, and in proportion as we may recognize its cause will be our insight into the true condition on which Parthenogenesis depends.

To this end we must revert to what takes place in the impregnated seed or ovum at the beginning of development, and duly ponder over the nature of the first steps in embryonic formation. These, observation has now established to be essentially the same in all organisms. The spermatozoon has been traced to the ovum in the lower Invertebrata and in Insects (where a special organ, the spermatheca, exists to ensure its application), in Mollusks, in Fishes, in Batrachians and up to the mammal. After

impregnation the germinal vesicle disappears and the germ-yelk (Pl. I. fig. 4, *a*) contracts. This constant effect of impregnation indicates the presence of an attractive force which has produced a certain condensation of the germ-yelk. If the yelk-membrane (*b*) were previously in contact with the chorion (*c*), it has now receded from it, and an albuminous fluid (*d*) occupies the interspace.

The primary germ-cell (*e*) soon appears at or near the centre of the germ-yelk. Its nucleus divides (fig. 5), and two germ-cells result; these recede and establish two centres of attraction and assimilative force, around which, in many species, the germ-yelk collects, and is thus divided (fig. 6). Each secondary germ-cell becomes two (fig. 7), and the matter of the germ-yelk is collected around four centres (fig. 8). The same process again takes place in each of these four, producing an eight-fold division, then a sixteen-fold one (fig. 9), and by its rapid repetition the germ-yelk becomes subdivided and assimilated into countless germ-cells (fig. 10), and by their further subdivision the nuclear or granular germ-mass (fig. 11) is established. This is the most common mode in which the primary impregnated germ-cell propagates itself at the expense of the germ-yelk. But in some species the germ-yelk is not attracted round the successively developed centres, but the germ-cells as they are propagated push their way through the germ-yelk and progressively assimilate it: the ultimate result being the same—a germ-mass of countless secondary germ-cells or nuclei. Much extraneous matter has been assimilated and combined with the essential matter of the primary impregnated germ-cell in order to form the material out of which the embryo is to be developed: but something more is done besides increase of bulk by assimilation and division.

The reception of the matter or principle of the spermatozoon by the germinal vesicle is essential to the commencement of this growth by multiplication of cells. When

the primary division of the impregnated germ-cell takes place, it must divide its properties with its matter between the two cells resulting from the spontaneous fission of its nucleus: and this result must follow every subsequent division *. It is scarcely figurative therefore to say that the primary or parent germ-cell has equally divided its spermatic virtue amongst its countless progeny.

What has here been propounded of the influence of the spermatozoon is equally applicable to the pollen-filament, and to those organisms in which the spermatic force has not been concentrated in matter presenting the common form of the spermatozoon or pollen-filament.

In the Polygastria, for example, the condition of spontaneous fission is due to the previous existence of a spermatic nucleus in each moiety which is about to be individualized.

* Professor Kölliker (Muller's Archiv für Physiologie, 1843, p. 137) has summed up the subordinate modifications of this constant and important preliminary process, as follows:—

The germ-cells are developed free in the yelk.

The first germ-cells are small and assimilate the yelk slowly.	The first germ-cells are large and take up the yelk quickly.
Yelk granular.	Yelk fluid.
Bothriocephalus. Ascaris dentata. Tænia. Oxyurus ambiguus. Distoma tereticolle.	*Cucullanus elegans.*

The germ-cells clothe themselves with the yelk.

The germ-cells clothe themselves with part of the yelk.	The germ-cells clothe themselves with the whole yelk (as in figs. 4–10, Pl. I.).
(Partial division.)	(Total division.)
Coregonus palæa.	*Rana. Triton.*
Alytes obstetricans.	*Lepus cuniculus.*
Sepia vulgaris.	*Canis familiaris.*
Loligo sagittata.	*Ascarides* permultæ.
	Strongyli nonnulli.
	Nereis. Botryllus.
	Pycnogonum. Æolidia.

The preliminary division of that nucleus has been constantly witnessed where the phænomena have been clearly traced. In many of Ehrenberg's beautiful plates the division of the nucleus is shown before that of the entire body of the monad has commenced; and according to the direction of the division of the nucleus, that of the monad has been either longitudinal* or transverse†. Two centres of assimilative

* See tab. 36. fig. 7. *Chilodon cucullulus*, 13, 14, 15.

† Ib. 16, 17, 18. Ehrenberg calls this nucleus of the Polygastria the 'testicle,' and views its division simply in the relation of the necessity of each individual resulting from the general fission having such an organ: meaning that each monad, developed by spontaneous fission, is perfected, as regards its so-called testis, by the spontaneous division of the previous testis, and not by the formation of a new one. But this is not the mode in which the eye, or the circle of teeth, or the pulsating sac, is gained by the second individual from the fission: the division usually takes place so as to include the original organ in one or in the other moiety; and that in which it may be wanting gets the organ by a special and independent development of it. The constancy of the preliminary fission of the nucleus would therefore show that it related rather to the totality of the act itself than to the partial completion of the individual in respect of its being provided with a particular male organ of generation. How then, we may inquire, does the division of the nucleus relate to the performance of the general act of spontaneous fission? Our hope of any insight into this mysterious relationship would be from some light to be derived by analogous phænomena. But with what phænomena is the one in question analogous? Obviously most closely with those which have been observed in the successive fissions of the impregnated germ-cell of those ova, such *e.g.* as the ova of the *Strongylus*, best adapted to give a view of the fission analogous to those which the perseverance of Ehrenberg enabled him to trace in the spontaneous fission of the monad.

The same correspondence between the successive generations of the *Chlamydomonas* and the formation of the germ-mass in the mammalian ovum has been well discerned and illustrated by Dr. Martin Barry, who has observed, "On examining the figures given by Ehrenberg of successive generations of the *Chlamydomonas*, I see a resemblance to the two, four, eight, &c. groups of cells in the mammiferous ovum too striking, not to suggest that the process of formation must be the same in both; the essential part of this process consisting in the division of the pellucid nucleus." See my 'Lectures on Invertebrata,' p. 24, 1843.

If this preliminary division of the germ-cell to the spontaneous fission

force have been set up in place of one, and the plastic power has arranged the organic matter around each of these centres, as it was around the single nucleus of which they are

of the germ-yelk has not been seen in the ova of other animals, it is because hitherto only the coarser phænomena of such division of the germinal body in Medusæ, Mollusca, Fishes, Frogs, &c. have been noticed. In Dr. Barry's observations however on the development of the germ-mass in the pellucid ova of the rabbit, phænomena closely analogous to those described by Siebold and Bagge in the ovum of the entozoon were detected.

In reflecting on the phænomena in the monad and the ovum—that a central something is first established, and the consequence of that —I have been led to draw the same conclusion with respect to both, and to regard the establishment of the special centre as the cause of the confluence of the parts around it; and I call it 'a centre of attractive and assimilative force.' Since the pellucid centre of the germinal body has not divided from the necessity of endowing the moiety to be separated by the subsequent fission with a particular organ required for its individual completeness, I infer that the same preliminary act in the monad was not solely for the purpose of providing its separated moieties with their respective testes, but that it had a higher significance.

As the pellucid centre in the ovum is the result of impregnation or of the reception of the matter of the spermatozoon, so it may be concluded that the nucleus of the monad is of a nature similar to, if not identical with, that of the spermatozoon. It was doubtless a gross view of its nature and analogies to regard it as the homologue of the whole preparatory organ of the spermatic fluid, such as is required in the higher animals; because as the germ-cells exist in the body of the Polygastria without the organ called ovarium, so we ought to expect that the essential matter of the sperm would likewise exist without a special testicular envelope.

The objection to Ehrenberg's determination of the nucleus as the 'testis,' that it has never been observed to produce spermatozoa, is akin to that which has been opposed to his determination of the ova, viz. that the young have never been seen to quit them and leave the shell behind. Neither of these objections will apply to the view of the nucleus as the essential matter of the sperm, and to the germ-cells as the essential elements of ova.

A filamentary spermatozoon is doubtless a very general form of the essential matter of the sperm: but in tracing the modifications of the spermatozoa from mammalia down the scale of animal life we find them gradually reduced to the head or nuclear part, and discern in the vibratile caudal appendage an accessory relating to the passage of the

the divisions. The same phænomena occur in the development of the cells during the growth of the conferval filament and of other cryptogamic plants.

fertilizing principle to the germ-cell, rather than to its essential operations when arrived there.

The best microscopical examinations of the spermatozoa show "that the spermatozoa are everywhere void of a special organization, and consist of an uniform homogeneous substance which exhibits a yellow amber-like glitter."—*Art.* SEMEN, *Cyclop. of Anatomy,* vol. iv. p. 502. The nucleus of the Polygastrian offers the closest resemblance to this character of tissue. And perhaps it may not be out of place here to notice the close analogy of the modification of form which the nucleus of some of the larger Polygastria, *Stentor Roeselii* e. g., presents to the spirally disposed elongated head of the spermatozoon in the Torpedo, Pelobates, and the Passerine birds.

The reception of the matter of the spermatozoon by the germ-cell is the essential preliminary to the primary processes of its spontaneous fissions: and when we see these fissions governed in the germ-cell of the *Ascaris* by the act of impregnation, followed by the appearance of a pellucid nucleus in the centre of the opake and altered germ-cell, and when we further see its successive fissions governed by the preliminary division of the pellucid centre, are we not naturally led to infer that that centre is the seat or the chief seat of the spermatic principle which the germ-cell has received? The mind must either be a mere passive recipient of these phænomena, or we must reason upon them and ask ourselves their meaning. The most probable signification of the appearance of the pellucid centre and of the initiative which it takes in the subsequent changes may be that which I have just explained: but this is certain, that the analogy between these phænomena in the multiplication of the parts of the germ-mass and those of the nucleus in the multiplication of the monads is so close, that one cannot reasonably suppose that the nature and properties of the nucleus of the impregnated germ-cell and that of the monad can be different.

Therefore I infer that the nucleus of the Polygastric Animalcules is the seat of the spermatic force: it can only be called 'testis' figuratively: it is the essence of the testis. It is the force which governs the act of propagation by spontaneous fission: and if Ehrenberg be correct in viewing the interstitial cell-corpuscles (körnchen) as germ-cells, these essential parts of ova may receive the essential matter of the sperm from the nucleus which is discharged along with them in the breaking up of the monad, which Ehrenberg regards as equivalent to an act of oviposition; and impregnated germ-cells may thus be prepared to diffuse through space and carry the species of Polygastric Animalcules

Wherefore it may be concluded that the presence of the spermatic force is essential to the process of growth by the multiplication of cells, and that the phænomena of the formation of the germ-mass are the provision for the presence of that force. It is only therefore a question of the degree of spermatic force which may suffice for any of the descendants of the primary impregnated germ-vesicle, in order to recommence and repeat the process to which the cell itself owed its origin. The result of such process would be always the same: the formation or accumulation of a germ-mass; that is to say, a mass of cells prepared as the materials upon which the plastic force might operate in the formation and adjustment of the different tissues and organs of a new individual.

What then might be expected to be the conditions of structure essential to the renewal of the process of forming a germ-mass in an individual organism, independently of the primal act of impregnation? Obviously the retention of some of the progeny of the primary germ-vesicle with their inherited spermatic virtue.

Now we have seen that the power of propagating by gemmation and spontaneous fission is in the ratio of the retention of germ-cells, as such, in the constitution of the individual first developed from the primary germ-mass. Plants are more cellular than animals; monads than rotifers; polypes than echinoderms; the tape worms than the round worms; the radiata than the articulata and mollusca; the invertebrata than the vertebrata.

to a distance from the scene of life of the parent. A very peculiar odour has always been recognized as one of the characteristics of the semen, which leads me to quote the following remark by Ehrenberg:— "Vast numbers of the *Euglena viridis*, dying contracted into a ball, form a delicate green pellicle on the water, which first exhales, as during life, a spermatic and then a mouldy odour: sinks during cold, rises during warmth, is decomposed into minute corpuscles and evolves gas, and the mass finally is resolved into a greyish dust which contains very minute ovules without chorion."

In proportion to the number of generations of germ-cells, with the concomitant dilution of the spermatic force, and in the ratio of the degree and extent of the conversion of these cells into the tissues and organs of the animal is the perfection of the individual, and the diminution of its power of propagating without the reception of fresh spermatic force.

In the vertebrate animal the whole of this force originally diffused amongst the cells or nuclei of the germ-mass is exhausted in the development of the tissues and organs of the individual, in the mysterious renovation of the spermatic power in the male by a special organ, and in the development of ova or cells prepared fit for its reception in the female. It now and then happens, even in the highest of Vertebrata—the human species—that an ovarian germ-cell sets up the process of embryonic development, but without sufficient of the spermatic and plastic power to complete even a larval form: some crude materials of the embryo are the sole result: teeth, it may be, or hair, with irregular amorphous ossifications, such as are met with occasionally in ovarian cysts.

The completion of an embryonic or larval form by the development of an ovarian germ-cell, or germ-mass, as in the Aphis, without the immediate reception of fresh spermatic force, has never been known to occur in any vertebrate animal.

The condition which renders this seemingly strange and mysterious generation of an embryo without precedent coitus possible, is the retention of a portion of the germ-mass unchanged. One sees such portion of the germ-mass taken into the semitransparent body of the embryo Aphis, like the remnant of the yelk in the chick. I at first thought that it was about to be inclosed within the alimentary canal, but it is not so. As the embryo grows it assumes the position of the ovarium, and becomes divided into oval masses and inclosed by the filamentary extremities of the

eight oviducts. Individual development is checked and arrested at the apterous larval condition. It is plain, therefore, that the essential condition of the development of another embryo in this larva is the retention of part of the progeny of the primary impregnated germ-cell.

What is really surprising in the phænomena of the Aphides is the potency of the mysterious virtue of the quintessential excretion, which sustaining so great a degree of subdivision, and of dilution with the material incorporated in the successive generation of cells, is nevertheless equal to the renewal and repetition of embryonic development through so many generations.

The explanation of the condition essential to this process is still more clearly afforded by the development of the *Distoma tarda* as described by Steenstrup. The entire impregnated ovum consists, as in most of the lower Invertebrata, of the germ-cells, which have assimilated the whole of the germ-yelk; the ovum, therefore, grows with the growth of the germ-mass which is formed by the usual processes of imbibition and spontaneous fission producing the multiplication of cells and nuclei: but certain of the outermost of these nuclei liquefy or coalesce, and form an additional layer to the chorion of a contractile or a ciliated structure. The ovum is thus transformed into a subelongate, subdepressed locomotive animal; which contains, however, nothing in its interior except the multiplied offspring of the primitive germ-cell. Here, therefore, we have the condition which I regard as essential to the development of an animal under circumstances which Steenstrup would define as 'alternate generation by the vital powers and by means of the bodies of the producing individuals,' and which the reviewer who has criticised him would prefer to call a development 'by a multiplication of cells by a process of continuous growth.' Neither of these definitions explain the condition to which I refer. That condition is the existence in each of the cell-progeny of the primary

germinal vesicle, of its share of that seminal virtue which was incorporated with the parent-cell in the act of impregnation and distributed by its successive divisions.

The course of development by which the ovum of the Distoma has been converted into the Gregariniform larva is as simple and as short as could be conceived, in order to support the idea of such a conversion. A free moving animalcular entozoon is, however, the result: a parasite closely resembling those of the genus *Gregarina* as defined by Kölliker and Siebold. This early larval form of the Distoma is explained to be a wet-nurse (*Amme*), or rather a grand-nurse (*Grosse-amme*), in the figurative language of Steenstrup. What it truly is, and what its powers are, and on what they depend, can only be understood by a recognition of the essential nature and signification of the first steps in its development, viz. the diffusion of the spermatic force in the formation of the germ-mass.

Now we might expect, from the analogy of higher animals, that certain of the constituent corpuscles of this germ-mass would perish as such in order to combine and form the tissues and organs of the Distoma. But the fertility of Nature's combinations and variations is inexhaustible! Instead of that ordinary process, several of the germ-corpuscles of the Gregariniform larva set up independently the centralizing actions of assimilation and spontaneous fission, and so constitute as many secondary germ-masses, in each of which a greater proportion of the constituent corpuscles coalesce and combine to form the tissues of an animal, like a Cercaria, than happened in the development of the Gregariniform parent. Under the form of Cercariæ these secondary larvæ, as they may be termed, burst the integument of the primary one and are set free; yielding one of the most striking examples of the multiparous character of the Trematode ovum; the multiplication of the larval forms which precede the ultimate oviparous individual being simultaneous, not consecutive as in the Aphis.

One witnesses something like this in the rapid development of the transverse segments of the *Strobila*, and their almost simultaneous liberation by spontaneous fission.

It would be needless to multiply the illustrations of the essential condition of these phænomena. That condition is, the retention of certain of the progeny of the primary impregnated germ-cell, or in other words, of the germ-mass unchanged in the body of the first individual developed from that germ-mass, with so much of the spermatic force inherited by the retained germ-cells from the parent-cell or germ-vesicle as suffices to set on foot and maintain the same series of formative actions as those which constituted the individual containing them.

How the retained spermatic force operates in the formation of a new germ-mass from a secondary, tertiary, or quaternary derivative germ-cell or nucleus, I do not profess to explain; neither is it known how it operates in developing the primary germ-mass from the impregnated germ-vesicle of the ovum. In both we witness centres of repulsion and of attraction antagonising to produce a definite result.

The physiologist congratulates himself with justice when he has been able to pass from cause to cause, until he arrives at the union of the spermatozoon with the germinal vesicle as the essential condition of development—a cause ready to operate when favourable circumstances concur, and without which cause those circumstances would have no effect.

What I have endeavoured to do has been to point out the conditions which bring about the presence of the same essential cause in the cases of the development of an embryo from a parent that has not itself been impregnated. The cause is the same in kind though not in degree, and every successive generation, or series of spontaneous fissions, of the primary impregnated germ-cell must weaken the spermatic force transmitted to such successive generations of cells.

The force is exhausted in proportion to the complexity

and living powers of the organism developed from the primary germ-cell and germ-mass. It is consequently longest retained and furthest transmitted in the vegetable kingdom; the zoophytes manifest it in the next degree of force; and the power of retained germ-cells to develope a germ-mass and embryo by the remnant of spermatic virtue which they inherited, is finally lost, according to our actual knowledge, in the class of Insects, and in the lower Mollusca. It is interesting, however, to observe this power energising, as it fades, in the reproduction of parts, *e. g.* the limbs of the lobster, when it is no longer capable of developing a whole.

The secondary circumstances attending such development of a germ-cell retained unaltered in the body, differ from those which attend the development of an ovum, and vary from one another as much as the accessory circumstances in the development of an ovum vary. An ovum is essentially a nucleated cell called the 'germinal vesicle,' with a granular fluid called the 'germ-yelk' in an envelope: it may contain a supplementary nutrient vitelline mass, properly called yelk, or a yelk with chalazæ and a calcareous shell, or a nidamental case and appendages of various kinds, &c., but the essential part is the germinal vesicle, and this cell must be impregnated. The ovaria and the conduits for the conveyance of the ovum outwards are superadded and accessory parts in the business of generation. An impregnated germ-cell imparts its spermatic power to its cell-offspring; but when these perish, or when the power is exhausted by a long descent, it must be renewed by fresh impregnation. But Nature is economical; and so long as sufficient power is retained by the progeny of the primary impregnated vesicle, individuals are developed from that progeny without the recurrence of the impregnating act.

The germinal vesicle is the essential part of an ovum.

An impregnated germ-cell is essential to the development

of the germ-mass and embryo *in ovo*: it is the primary impregnated germ-cell.

A derivative germ-cell, the progeny of the primary one, retaining a due amount of spermatic force, is essential to the development of a secondary germ-mass and embryo within the body of the primary one.

The gregariniform larva, or locomotive ovum, of the *Distoma tarda* exemplifies the above propositions and plainly illustrates the essential condition of its Parthenogenesis, or power of propagating 'sine concubitu.'

Were any one to assert that the development of the cercariform larva from one of these secondary germ-masses was altogether distinct from the development *ab ovo*, by being 'a multiplication of cells by a process of *continuous growth**,' we could regard such assertion in no other light than as a purely arbitrary one, and as betraying a want of appreciation of what must be effected when the primary impregnated germ-cell subdivides itself into the secondary ones in order to form the germ-mass.

Reverting again to the gregariniform larvæ, let us suppose that besides the cells of the germ-mass of the ovum of the Distoma which have perished as such to form the larval integument, others had coalesced to constitute special envelopes of parts of the unchanged germ-mass, and to form canals leading from those ovarian envelopes outwards: if any of such included germ-masses set on foot the processes of forming an embryo, such embryo would be excluded 'per vaginam' as in the Aphis, instead of bursting through the integument as in the gregariniform entozoal larva.

* The reverse of this idea is so obvious, that the veritable correspondence between ovulation and gemmation could not escape the notice of the equal observer of nature. Dujardin alludes to the common recognition of it in his 'Memoir on the Infusoria':—'Les gemmes, les bourgeons qu'on voit se détacher du corps des zoophytes peuvent encore être comparés jusqu'à un certain point avec les germes détachés de l'ovaire des animaux plus parfaites."—*Annales des Sciences Nat.* 1838, p. 290.

Or let us suppose that certain other germ-cells in that larva were to combine and coalesce to form a stomach, and to push out prehensile arms around its mouth, pressing the retained germ-cells into the substance of the thickened integument, or aggregating them near the base of the stomach: if any of such germ-cells were to set on foot the process of forming a germ-mass, it might protrude outwards, as in the Hydra, and the embryo might include the stretched portion of integument of the parent in the progress of its development.

But this development by gemmation would differ from that *ab ovo* only in accessory and non-essential particulars; the nature of the essential spermatic force would be the same.

Such is the explanation which I have to offer of the phænomena which meet us at the outset of our inquiries into the generation of animals, and which I have grouped together under the term 'Parthenogenesis.' These phænomena have hitherto remained the most obscure and seemingly anomalous in the chapter of Comparative Physiology relating to Generation; but, with this understanding of their nature, they appear to me to enter into the ordinary laws of the function, and to be disguised only by accessory and non-essential modifications. Had I indeed, in the place of such explanation, deduced from observation of the first steps in development, salved these phænomena by the proposition "that they took place agreeably with the law of alternate generation;" "by the vital powers and by means of the bodies" of the producing individuals; and had I applied to the cercarial larva of the Distomata, to the polypoid larva of the Medusæ, and to the apterous larva of the Aphides, the metaphorical phrase of 'wet-nurses' and 'nursing-generations,' I should have succeeded in concealing my own ignorance of the organic conditions essential to these remarkable reproductive processes, in the

same degree in which such propositions and phrases might have seemed or sounded to you like explanations of the facts: but I should have done no more: you would have had apparent instead of real knowledge.

No one, as it appears to me, who carefully analyses the language of the Generations-wechsel theory of Professor Steenstrup, will be able to conceal from himself that it conveys no idea leading, even by a single step, to a closer knowledge of the essential conditions of the development of an *Aphis* in the body of a virgin parent. But all will readily concede to him the merit of the assemblage of the phænomena from scattered memoirs into one convenient work, and gratefully award to the ingenious author the praise due for this useful labour, as well as for the confirmation of some of the facts and the addition of others, which yet must have remained as unexplained and empirical phænomena, until the organic conditions had been pointed out which are essential to the 'Lucina sine concubitu.'

THE END.

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